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THE POLYPORACEAE OF IOWA

by

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THE POLYPORACEAE OF IOWA

The Polyporaceae includes those Hymenomycetes in which the hymenial layer covers the surface of pores, pits or anastomosing folds. These may be cylindric hollow tubes, honeycomb-like pores, anastomosing passages or, rarely, concentric or radiating lamellae. The sporophore may be sessile or stipitate, if sessile, applanate or resupinate; it may vary in texture from fleshy to coriaceous, corky, woody, membranous or even gelatinous. The basidia are usually four spored, and the spores vary in size, form and color. The fructification may be either annual or perennial.

The fungi belonging to the family Polyporaceae include a large number of wood-rotting species, ranging from purely saprophytic forms through nearly all degrees of parasitism. They may be found inhabiting stumps, logs, fallen tree trunks, piers and posts, as well as growing on the ground, and a number attack structural timbers. Once the mycelium becomes established, the fungus spreads and the wood is gradually digested, thus parasitic species may cause the death of living trees.

The mycological herbarium of the State University of Iowa contains the collection on which the following study was based. This material has been accumulating during a period of over forty years and includes all of the common species represented in the state as well as a number of the rarer species. The collections contain numerous specimens gathered by Professor Thomas H. Macbride and Professor Bohumil Shimek, dating back to the '80's, and more recent collections made by Professor George W. Martin and others associated with him in mycological work. These specimens were studied, and the determinations checked; careful drawings were made of spores and other characteristic structures. Undetermined specimens were also studied and named by the writer wherever possible. Species previously reported from Iowa but not contained in the herbarium have been included in the keys.

This study was suggested by Professor George W. Martin, and the work was carried on under his direction in the Department of Botany of the State University of Iowa.

Overholts' Polyporaceae of the Middle-Western United States(34) is the most useful treatment of the polypores occurring in the region of which Iowa is a part, and this work has been drawn upon freely in the preparation of the present paper. The genus *Poria* and the *Boleteae*, not treated by Overholts in his paper, are included in the present work. Other papers which have been used extensively are Macbride, Saprophytic Fungi of Eastern Iowa(20), one of the first papers on the Polyporaceae of Iowa; Burt, *Merulius* in North America(5); Murrill, Northern Polypores(27), American *Boletes*(28), and North American Flora, Vol. 9(26); Overholts, Species of *Poria* described by Peck(37); Neuman, Polyporaceae of Wisconsin(32); Fennell, The Polyporaceae of Iowa(8). Other references are cited in the bibliography.

The family is a large one and includes diversified forms. It is to some extent artificial, containing species which merge with the agarics through *Lenzites* on the one hand, and on the other with the *Hydnaceae* as represented by *Phlebia*, which may be regarded as closely related to *Merulius*.

In studying microscopic characters of spores, setae, cystidia and hyphae, free-hand sections were made and transferred directly to the slide into a drop of Amann's medium which had the effect of expanding the hyphae to their normal size. In most cases the sections were cut dry but in some cases the piece to be sectioned was first moistened with alcohol and water.

Drawings were all made to a common magnification ($\times 1675$) using the camera lucida with Zeiss $\frac{1}{12}$ " oil immersion objective and 10x ocular.

The family is here divided into the four natural tribes: *Merulieae*, *Fistulineae*, *Polyporeae*, and *Boleteae*. The tribes, *Merulieae* and *Fistulineae* are represented each by a single genus, *Merulius* and *Fistulina* respectively. The largest tribe, *Polyporeae*, contains the greatest number of genera, eleven in all, as follows: *Poria*, *Gloeoporus*, *Trametes*, *Cyclomyces*, *Lenzites*, *Daedalea*, *Favolus*, *Ganoderma*, *Fomes*, *Polystictus*,

Polyporus. The tribe Boletéae contains three commonly accepted genera: Boletus, Boletinus, and Strobilomyces.

The genus Solenia is sometimes included in the Polyporaceae but since its relationship seems rather to be with the Thelephoraceae, following Burt(4) it is here excluded.

KEY TO TRIBES OF POLYPORACEAE

- a. Hymenium not distinctly poroid, borne on the surface of shallow pits, or weak, anastomosing veins or folds-----I. Merulieae
- a. Hymenium distinctly poroid, or covering lacerated teeth, or concentric or radiating anastomosing lamellae-----b
 - b. Hymenial cavities tubular, each tube separate and distinct from every other -----II. Fistulineae
 - b. Tubes firmly grown together-----c
- c. Hymenophore tough or woody, rarely fleshy; tubes usually not separable as a layer from the context-----III. Polyporeae
- c. Hymenophore fleshy throughout, putrescent; tubes usually separable in a layer from the context-----IV. Boletaeae

Tribe I. Merulieae

Sporophore resupinate or reflexed; hymenial layer shallow pitted, at first with a moldy appearance; the pits formed by soft low anastomosing folds.

A single genus.

Genus MERULIUS Haller ex Fr.

Sporophore soft and watery to dry and coriaceous; resupinate or sometimes dimidiate or effused-reflexed when best developed; epixylous, rarely on earth or brick walls; hymenophore gelatinous, sub-gelatinous, waxy, membranaceous or floccose, consisting of anastomosing folds forming shallow, irregular and often sinuous pores, sometimes obsoletely toothed, especially on drying; edges of pits or pores fertile; spores white to ochraceous; basidia simple.

KEY TO SPECIES OF MERULIUS

- a. Fructification always resupinate -----b
- a. Fructification effused-reflexed when best developed but sometimes occurring resupinate -----c
 - b. Fructification adnate; drying ochraceous cream-buff to pinkish buff, rarely paler, often cracking and flaking away; pores 4-6 per mm.; spores hyaline -----1. *M. ceracellus*
 - b. Fructification not adnate, but separable from the substratum; hymenium drying very dark brown, Brussels brown to bone-brown, with folds becoming raduloid teeth on an inclined

- surface; pores 1-1.5 mm. in diameter; spores dark brown in spore collection, $9 \times 6\mu$ -----2. *M. americanus*
- c. Spores ferruginous or ochraceous in mass; fructification large, 2-10 mm. or more thick when fresh, spongy-fleshy; hyaline and colored hyphae in subhymenial layer, spores citron-yellow under microscope -----3. *M. lacrymans*
- c. Spores hyaline -----d
- d. Fructification fleshy tremellose when fresh, or walls of hyphae of subhymenial layer gelatinously modified-----e
- d. Fructification not fleshy tremellose when fresh-----g
- e. Fructification with subhymenial layer having walls of its hyphae gelatinously modified, but thin and somewhat pliant when dry; no cystidia; spores $4-5 \times 2-2.5 \mu$ -----4. *M. ambiguus*
- e. Fructification fleshy tremellose; drying hard and horny so that it requires several minutes to absorb water-----f
- f. Hymenium dark garnet red, sometimes flesh-pink-----5. *M. incarnatus*
- f. Hymenium not dark garnet red but ruddy, somewhat translucent, drying cinnamon-buff and prussian-red--6. *M. tremellosus*
- g. Hyphae of subhymenial layer incrustated; fructification coriaceous, soft, reflexed portion tomentose, concentrically sulcate when broadly reflexed, white to pallid neutral gray; spores $4.5-5 \times 2.5 \mu$ -----7. *M. confluens*
- g. Hyphae not incrustated, reflexed portion white, villose, soft, thin; pores drying pinkish-buff to cinnamon; about 3 per mm.; spores $4.5-5 \times 1.7-2.5 \mu$ -----8. *M. corium*

1. *M. ceracellus* Berk. and Curtis

Fig. 1

Fructification entirely resupinate, adnate, thin, margin thin, whitish, 2-5 cm. long, 1-2 cm. broad; hymenium drying ochraceous cream-buff to pinkish buff, rarely paler, even at first, becoming minutely pitted, pores 4-6 per mm., very shallow, forming more or less anastomosing folds, cracking and sometimes flaking away from substratum on drying; subiculum cotton-like, very thin, $60-200 \mu$, folds projecting 140μ ; hyphae hyaline, interwoven, $2-3 \mu$ in diameter, not incrustated, not usually nodose septate; cystidia none; spores hyaline, smooth, $4-4.5 \times 1.5-2 \mu$.

On under side of decaying limbs of oak, linden, and other deciduous trees.

Our specimens agree in every point except that in some there are clamp connections on the hyphae.

2. *M. americanus* Burt

Fig. 2

Fructification resupinate, effused, membranous, thin, fragile, separable, dry, drying dark brown; margin thin, 3-15 cm. in diameter; hymenial layer gyrose-porose, folds growing out into raduloid teeth on an inclined surface; pores 1-1.5 mm. in diameter, up to 1.5 mm. deep; subiculum of two layers, one next to the substratum composed of loosely interwoven, rigid, nodose-septate, colored hyphae 4.5-6 μ in diameter, and hyaline sometimes granular-incrusted hyphae intermixed, the other layer narrow, bearing the hymenium, composed of densely arranged hyaline or nearly hyaline hyphae; cystidia none; spores yellowish-brown, smooth, 9 x 6 μ .

Coniferous logs and boards in moist places. Rarely on deciduous wood. Common.

3. *M. lacrymans* Wulfen ex Fries

Fig. 3

Fructification resupinate, effused-reflexed, or producing large stalked tubercles from a median placenta, thick, large, spongy-fleshy, moist, yellow-ferruginous, drying dark brown to warm sepia, margin tomentose, white; 8-15 cm. in diameter, up to 1 cm. or more thick when fresh; hymenium porose, gyrose-dentate, pores large, 1-2 mm. in diameter, up to 2 mm. deep, dissepiments later growing into raduloid teeth; subiculum 2-10 mm. thick, densely interwoven, hyphae nodose-septate, either colored like spores or hyaline, thick-walled, 5-6 μ in diameter, or hyaline, 3.5-4.5 μ , septate with clamp connections; cystidia none; spores citron-yellow under microscope, warm sepia in spore collection, smooth, elliptical, 9-10 x 5-6 μ , somewhat flattened on one side, 1-guttulate.

On coniferous logs, or structural timbers. Rarely on stumps, or on the ground. Rare. The collections so reported seem usually to be *M. americanus*.

4. *M. ambiguus* Berkeley

Fructification orbicular, sometimes resupinate, usually narrowly reflexed, coriaceous-soft, tomentose, often concentrically sulcate, whitish to smoke-gray when dry, 2-6 cm. broad; hymenial layer tawny olive to Rood's brown when dry, folds

radiate, flexuous and branching, later transversely connected and forming shallow, angular pores about 1×0.5 mm.; subiculum of two layers, the layer next to substratum composed of loosely interwoven hyaline hyphae, $50-100 \mu$ thick, and a gelatinous, broader layer bearing hymenium; spores hyaline, smooth, $4.5 \times 2-2.5 \mu$.

On coniferous logs.

This species is reported from Iowa by Fennell. No specimen, however, is contained in the State University of Iowa Herbarium.

5. *M. incarnatus* Schw.

Fig. 4

Fructification effused-reflexed, fleshy tremellose, reflexed portion tomentose, pallid with age; hymenial layer flesh pink to garnet red, in Ridgway as garnet brown and Hessian brown, pores radially elongated, transversely venose and subdivided into smaller angular pores; subiculum $0.5-2$ mm. thick, composed of hyaline septate hyphae, $2.5-5 \mu$ in diameter, with clamp connections; spores hyaline, smooth, $1 \times 3-4 \mu$; cystidia incrustated or unincrusted if present, $5-7 \mu$ broad, projecting $10-25 \mu$.

On stumps and logs of deciduous trees.

6. *M. tremellosus* Schrader

Fig. 5

Fructification resupinate, reflexed, or effused-reflexed, fleshy-tremellose, upper surface tomentose, white, $2-6$ cm. in diameter, reflexed margin up to 1.5 cm. broad, sometimes imbricate; hymenial layer ruddy, somewhat translucent, cinnamon-buff to Prussian red (Ridg.) when dry, pores shallow to rather deep, radially elongated, $1-1.5 \times 0.5$ mm., transversely venose, finally subdivided into smaller, equal, angular pores; subiculum $0.5-2$ mm. thick, composed of a layer next to substratum, of loosely interwoven hyphae, $3-4 \mu$ in diameter, and a broad gelatinous layer, composed of densely arranged, parallel, hyaline hyphae with walls gelatinously modified; cystidia incrustated or unincrusted, sparingly present, $3.5-4.5 \mu$ in diameter, projecting $15-25 \mu$ above basidia; spores hyaline, smooth, allantoid, $3-4 \times 0.5-1 \mu$.

On decaying logs and stumps of deciduous trees, rarely on coniferous logs. Very common.

7. *M. confluens* Schw.

Fig. 7

Fructification resupinate, longitudinally effused, coriaceous, soft, thin, margin free, inflexed, subtomentose, shallowly concentrically sulcate when broadly reflexed, white to pallid or gray when dry, 1-4 cm. in diameter, 4-10 cm. long, usually laterally confluent on a horizontal surface, reflexed portion 1-10 mm broad; hymenial layer drying pinkish cinnamon to pecan brown, reticulately porose, shallow, 2-4 pores per mm., 300-500 μ thick, of loosely interwoven hyaline hyphae near the hymenium; subiculum composed of loosely interwoven hyaline hyphae. 3-5 μ in diameter, incrusting near the hymenium; cystidia none; spores hyaline, smooth, cylindric, flattened on one side, 4.5-5 x 1-2.5 μ .

On bark of dead branches of alder, rare on conifers.

8. *M. corium* Fr.

Fig. 8

Fructification resupinate, effused, coriaceous, thin, margin finally free, reflexed, surface of reflexed portion villous, white; hymenium reticulately porose, drying pinkish buff to cinnamon, 1-4 cm. in diameter to 6 cm. long; pores about 3 per mm., shallow; subiculum 300-500 μ thick, composed of loosely interwoven hyaline hyphae 3-4 μ in diameter, hyphae not incrusting, with no clamp connections; no cystidia; spores hyaline, smooth, cylindric, 4.5-5 x 1.7-2.5 μ .

Rare.

Tribe II. *Fistulineae*

Sporophore at first verrucose on lower surface, the warts later developing into peg-like tubes which are open at the lower end, hymenium lining the inner surface of the tubes, each tube being distinct from the others; context soft and watery; basidia with four sterigmata; spores brown.

A single genus.

Genus *FISTULINA* (Bull.) Fr.

Hymenophore composed of cylindric tubes on the lower sur-

face of a fleshy pileus; tubes remain free from each other, pileus somewhat fleshy.

A single species in Iowa.

1. *F. hepatica* (Huds.) Fr.

Pileus dimidiate, or subspathulate, substipitate or attached by a broad base; thick, fleshy, soft, surface somewhat viscid, fibrous, variegated to blood-red; context white; tubes short, cylindric, crowded, but very distinct, at first pallid, then red to chestnut brown when dry; spores hyaline under microscope, salmon color in mass, smooth, broadly elliptical, 4-5 x 2.5-3 μ ; cystidia present.

Not common.

Tribe III. Polyporeae

Sporophore stipitate, applanate, effused, effused-reflexed, or sometimes resupinate; texture coriaceous, corky, woody, membranous, subfleshy or rarely fleshy; substance of the context firmly attached to the hymenial layer, thus usually not easily separable from the context; pores typically cylindric or angular, varying to honeycomb-like cells, sinuous labyrinthiform chambers, concentric or radiating anastomosing lamellae; basidia four-spored, spores varying in form and color.

KEY TO GENERA OF POLYPOREAE

- a. Sporophore entirely resupinate *Poria*
- a. Sporophore pileate; sessile or stipitate, sometimes effused-reflexed...b
 - b. Tubes waxy, separable, texture of pileus somewhat gelatinous when moist *Gloeoporus*
 - b. Tubes not waxy, rarely separable, texture of pileus coriaceous to woody, rarely somewhat fleshyc
- c. Context continuous with trama, hence layer of tubes not separable from upper part of pileus; tubes generally sunken at unequal depths into context *Trametes*
- c. Context and trama of different textures; often separated by a definite boundary; tubes usually sunken at equal depthsd
 - d. Hymenium borne on concentric lamellae; pileus usually stipitate *Cyclomyces*
 - d. Hymenium not borne on concentric lamellaee
- e. Hymenium covering surface of radiating lamellae which usually anastomose *Lenzites*
- e. Hymenium not lamellatef
 - f. Hymenium covering surface of labyrinthiform folds or passages, sometimes breaking up into teeth in older portions. *Daedalea*

- f. Hymenium not labyrinthiform -----g
- g. Pores hexagonal in shape, or honeycomb-like radiating from a lateral or central stipe, and longer in the radial direction-----Favolus
- g. Pores circular to angular-----h
 - h. Surface of pileus lacquered, annual or perennial---Ganoderma
 - h. Surface of pileus not lacquered, sometimes incrustated-----i
- i. Sporophore perennial, forming a new layer of tubes each year, or more often -----Fomes
- i. Sporophore annual, forming only a single layer of tubes-----j
 - j. Sporophore thin coriaceous or membranous-----Polystictus
 - j. Sporophore tough, coriaceous, corky, woody, sometimes fleshy or subfleshy -----Polyporus

Genus PORIA (Pers.) Fr.

Fructification entirely resupinate, effused; texture membranous, fleshy, coriaceous or woody; pores round, angular, sinuous, labyrinthiform, dentate or lacerate; often placed immediately upon the wood or mycelium without an interposed subiculum; spores usually hyaline and smooth, formation of pores precedes formation of hymenium, lacking a hymenium on the edge of the dissepiments when mature.

KEY TO SPECIES OF PORIA

- a. Fructification white, pallid or pale tinted-----b
- a. Fructification distinctly colored, usually dark-----p
 - b. Fructification usually remaining distinctly white on drying---c
 - b. Fructification not as above-----d
- c. Growing on the ground-----1. *P. terrestris*
- c. Growing on decayed coniferous wood, or on charred wood-----
 - 2. *P. sericeo-mollis*
 - d. Pores becoming yellowish, pallid or cream colored, white or whitish at first -----e
 - d. Pores yellow, pinkish cinnamon, pinkish buff, pinkish ochre or lilac tinted when fresh -----o
- e. Pores minute -----f
- e. Pores medium or large -----l
 - f. Spores globose or nearly so -----g
 - f. Spores not globose -----h
- g. Surface of pores roughened by unequal prominent tubercles, averaging 3-3.5 per mm. -----3. *P. subacida* var. *tuberculosa*
- g. Surface of pores smooth, averaging 3-5 per mm., pores white, yellowish or cream colored -----4. *P. medulla-panis*
 - h. Pores very short, 0.5 mm. long or less-----i
 - h. Pores longer than above -----j
- i. Pores grayish-white when fresh, spores cylindric, 4-5 x 1-2 μ -----
 - 5. *P. griseoalba*

- i. Pores whitish, pale cream-colored or light vinaceous when fresh, spores oval, $2.5-4 \times 2 \mu$ -----6. *P. semitincta*
- j. Hyphae with clamp connections present, ends of hyphae bulb-like -----7. *P. mucida*
- j. Hyphae not as above -----k
- k. Margin smooth -----8. *P. vulgaris*
- k. Margin byssoid, radiately fibrillose -----9. *P. mollusca*
- l. Growing on pine, spores large, $5.5-7 \times 4-5 \mu$ -----10. *P. pinea*
- l. Not growing on pine generally -----m
- m. Spores large, characteristically with one conspicuous guttule, cystidia absent -----11. *P. radiculosa*
- m. Spores not guttulate as above -----n
- n. Spores large, adhering in groups, cystidia present, hyphae with cross walls distinct, but without clamp connections -----12. *P. corticola*
- n. Spores not adhering in groups, cystidia absent, hyphae without clamp connections -----13. *P. vaporaria*
- o. Margin fimbriate with a few fine rhizomorphic strands, pores white or lilac tinted -----6. *P. semitincta*
- o. Margin not fimbriate, slightly pubescent, pores pinkish ochre to light buff, pinkish cinnamon or light ochraceous salmon when fresh -----14. *P. attenuata*
- p. Pores dark or rich salmon colored when fresh, becoming faded when dry, hyphae branched, spores $5.5-8 \times 3-5 \mu$ -----15. *P. salmonicolor*
- p. Pores not rich salmon color when fresh -----q
- q. Pores having a resinous appearance when dry, very small, 6-7 per mm.; hymenium not developed, pores orange-buff to ochraceous orange when fresh, dark red when dry -----16. *P. spissa*
- q. Not as above -----r
- r. Pores brown or black -----s
- r. Pores not brown or black -----x
- s. Fructification distinctly black; hyphae dark brown -----17. *P. nigra*
- s. Fructification not black -----t
- t. Pores yellowish-brown; margin paler and distinctly hirsute, barbate -----18. *P. barbaeformis*
- t. Not as above -----u
- u. Cystidia present -----v
- u. Cystidia not present; pores very small, 7-9 per mm. -----19. *P. punctata*
- v. Cystidia short, $10-15 \times 5 \mu$; pores oblique, hyaline network of subhymenial hyphae; spores $4-4.5 \times 2-2.5 \mu$ -----20. *P. obliqua*
- v. Cystidia longer than above -----w
- w. Cystidia very long, projecting, $25-40 \mu$, spores cylindric, $6-7 \times 2 \mu$; pores occasionally more or less daedaloid -----21. *P. viticola*
- w. Cystidia not as long, projecting $15-30 \mu$; spores not quite as long as above, $4.5-5 \times 2-3 \mu$; pores never daedaloid -----22. *P. ferruginosa*
- x. Subiculum brown, 1-5 mm. thick, much thicker than the tubes;

- mouths of pores drab, wood brown or with a grayish pruinosity -----23. *P. setigera*
- x. Subiculum not brown; fructification not as above-----y
- y. Pores red, small, thin walled-----24. *P. rufa*
- y. Pores not red -----z
- z. Margin fimbriate, with a few fine rhizomorphic strands, pores white or lilac tinted -----6. *P. semitincta*
- z. Margin not fimbriate, slightly pubescent, pores pinkish ochre to light buff, pinkish cinnamon or light ochraceous salmon when fresh -----14. *P. attenuata*

1. *P. terrestris* (DC.) Fr.

Fig. 7

Fructification effused on the ground, uneven, thin, separable, annual, white or whitish, moist, irregular in outline; margin sterile, rather wide, pubescent, irregular; pores 1-2 mm. long, mouths angular to round, white, shallow, sunken at unequal depths into context, smaller toward margin, averaging 2-4 per mm.; spores hyaline, smooth, subglobose, 4-5 x 3-4 μ ; hyphae hyaline, byssoid, evanescent, 2.5-4 μ broad, rhizomorphic strands abundant and prominent, penetrating ground in various directions.

On earth walls, in greenhouses, etc.

The two specimens in the State University of Iowa Herbarium were found growing on the ground in the greenhouse, one in October, 1928, the other in October, 1929.

2. *P. sericeo-mollis* Romell

Fig. 8

Fructification effused, soft, uneven, white, remaining so when dry, margin finely tomentose also below where raised up from substratum, separating, thin at edge, thicker in center, 0.5-3 mm. thick; pores 3-4 per mm., not more than 3 mm. long; mouths round to angular, growing obliquely, white, at length cream or pallid; spores hyaline, 4-6 x 2-3 μ , many found in dried specimens; basidia 5 μ broad, 4-spored; hyphae hyaline; clamp connections present, 2-5 μ broad; cystidia incrustated at top, abundant, 5 x 15 μ .

On rotten coniferous wood.

The specimen studied was on a charred log.

3. *P. subacida* (Peck) Sacc.

Fig. 12

Fructification effused, annual, separable from substratum except perhaps on an uneven surface; sterile tomentose margin, 5-6 mm. broad, narrow, and almost disappearing in mature specimens; subiculum very thin, white; pores 2-4 mm. long when well developed, shorter at times or longer in oblique position; mouths whitish or light yellow, pinkish buff to avellaneous when dry, angular or rounded, 3-3.5 per mm.; dissepiments thin but entire; spores hyaline, smooth, ellipsoid or oblong ellipsoid, sometimes obliquely apiculate, $4.5-6 \times 2-4 \mu$; cystidia clavate, thickened at apex, very hard to find, $5-7 \mu$ in diameter; hyphae unbranched, hyaline, no cross walls or clamp connections, in trama hyphae are compacted parallel to each other, $4-6 \mu$ in diameter.

On trunks and decaying wood of various trees.

The variety *tuberculosis* is in the State University of Iowa Mycological herbarium. "It has the surface roughened by unequal prominent tubercules, which are scattered or clustered. They appear to be a monstrous development of the mycelium on the surface of the pores." (Overholts.) This species is very close to *P. medulla-panis*, especially in microscopic characters.

4. *P. medulla-panis* (Pers.) Cooke

Fig. 9

Fructification effused, often for many centimeters, adnate or separating only with difficulty, annual or reviving for several years, typically with a pubescent or tomentose margin, white to cream buff, becoming yellowish; subiculum a very thin pallid layer almost disappearing in older specimens; pores 0.5-3 mm. long each season; mouths pure white, wood colored to egg yellow, circular, with dissepiments thick, to angular with dissepiments thinner, always entire, often oblique, averaging 3-5 per mm., finally indistinctly stratified in three or four layers or sometimes distinctly so with a thin layer of context separating each tube layer; spores hyaline, smooth, ellipsoid to oblong-ellipsoid or broadly ellipsoid, $4-6 \times 3-4.5 \mu$; basidia broadly clavate to pyriform, 5-8 μ broad; cystidia

none or represented by pointed fusoid hyaline paraphysis-like bodies; large crystals present in trama; hyphae variable, much branched or unbranched, 1.5-5 μ in diameter, no cross walls or clamp connections.

On bark and wood of deciduous trees. Often on fence posts or structural timbers. Common.

This species varies from a thin, compact, rather hard form to a coriaceous or leathery form, more or less separable from the substratum.

P. pulchella Schw. is considered the yellow form of *Poria medulla-panis*.

Syn.: *P. xantholoma* Schw.; *P. xantha* Schw.

One specimen in the herbarium collected by Holway and labeled *Poria obducens* seems to be the same as *P. medulla-panis*. The only apparent difference is that there seems to be more than one layer of tubes in *P. obducens*.

5. *P. griseoalba* (Peck) Sacc.

Fig. 20

Fructification not widely effused, inseparable, indeterminate, very thin, fertile to margin, annual; subiculum not visible when dry; pores less than .25 mm. long, mouths grayish-white when fresh, pinkish-buff or cinnamon-buff when dry, circular, thin-walled, entire, averaging 4-6 per mm.; spores hyaline, smooth, oblong or short cylindric, sometimes allantoid, 4-5 x 1-2 μ ; basidia 2-3 μ in diameter, often arising in a series from one side of a hypha in the hymenial region; hyphae hyaline, 5-7.5 μ in diameter, made up of short cells, others 2.5-5 μ broad and longer, branching, anastomosing and usually slightly incrustated, no clamp connections, septate.

On well-rotted wood of deciduous trees.

6. *P. semitincta* (Peck) Cooke

Fig. 13

Fructification generally not widely effused, thin, separable from substratum, annual, sterile margin, from which a few fine rhizomorphic strands are rarely produced, white or with a tinge of lilac; subiculum very thin, soft, cottony, noticeable on the margin; pores as shallow depressions, less than 0.5 mm. long, meruloid in dried specimens, whitish or pale-cream

color when fresh, avellaneous to pinkish cinnamon when dry, or a light vinaceous shade rarely persisting, mouths sub-rounded, averaging 3 per mm., dissepiments thin, entire, often uneven, more or less toothed on the edges; spores hyaline, smooth, oblong, $2.5-4 \times 1-2 \mu$; basidia $2-3 \mu$ broad; cystidia present or absent, when present long and incrusting; hyphae hyaline, flexuous and loosely arranged, branching, $4-7 \mu$ in diameter, cross walls present, clamp connections absent.

On wood of deciduous trees, sometimes on leaves.

7. *P. mucida* (Pers.) Fr.

Fig. 10

Fructification effused, rather thick up to 5 mm., somewhat immersed, soft, white, becoming pallid; margin uneven, byssoid; pores 1-3 per mm. medium, angular, unequal, lacerate, received in a crustaceous mycelium, dissepiments thin; spores hyaline, ellipsoid, $4-6 \times 2.5-3 \mu$; hyphae hyaline, with small rather abundant clamp connections, with bulb-like ends.

On rotten deciduous wood.

Syn. *Irpex sinuosus* Fr.; *Poria sinuosus* Fr.; *Poria radula* (Pers.) Fr.; *Irpex obliquus* (Schr.) Fr.

These names have been applied in this country. Europeans do not agree on the uses of any of them. Probably our commonest *Poria* on hardwoods. This species is closely related to *P. mollusca*.

8. *Poria vulgaris* Fr.

Fructification broadly effused, thin, dry, closely adnate, inseparable; subiculum very thin; pores about one mm. long, mouths white or yellowish, small, round, nearly equal, sometimes oblique, 5-6 per mm.; hyphae of hymenium hyaline, undulate, $2-4 \mu$ broad.

On dead wood and branches of deciduous trees.

Spores were not seen in the specimen studied but numerous conidia were found which measured $2-4 \times 4-5 \mu$.

9. *P. mollusca* (Pers.) Fr.

Fructification effused, thin, soft, white, sometimes yellowish; margin white, byssoid, radiately fibrillose; pores white, thin, pale ochraceous, 0.5-1 mm. long, developing from vari-

ous centers, small, thin, round unequal, torn; spores hyaline, smooth, subglobose, $4 \times 3.5 \mu$.

On stumps and dead branches of conifers. Macbride has also reported it as occurring on *Salix*.

10. *P. pinea* (Peck) Sacc.

Fructification annual, effused for several centimeters, rather tender, separable, margin sterile, thin, white or yellowish when young, disappearing when older; subiculum very thin, whitish and distinct; tubes 2-6 mm. long, dingy white when fresh, becoming very much darker on drying, fuscous in herbarium specimens; mouths rather large, 2-1.5 per mm., angular, thin walled; spores hyaline, smooth, ellipsoidal or oval, $7.5-11 \times 4-7 \mu$ when mature, $5.5-7 \times 4-5 \mu$ immature; cystidia none; hyphae hyaline, thin walled, a few cross walls, sparingly branching, $1-3 \mu$ in diameter.

On wood and bark of pine.

11. *P. radiculosa* (Peck) Sacc.

Fructification annual, effused, thin, soft, tender, margin of white tomentose mycelium creeping in and over the wood; subiculum of a very thin membrane of interwoven mycelia; pores rather large, at first white then yellow, angular, at first shallow, sunken in mycelium, becoming 1-4 mm. long, dissepiments thin and fragile; spores hyaline, smooth, elliptical, characteristically one guttulate, $5-7 \times 2.5-4 \mu$; cystidia none; hyphae hyaline, branching, with rather conspicuous clamp connections and cross walls, in the subiculum some of the hyphae are slightly granular in appearance, $4-7 \mu$ in diameter.

The specimen studied was found on a coniferous plank.

12. *P. corticola* (Fr.) Cooke

Fructification broadly effused for several centimeters where best developed, adnate when young, separable when mature, soft and watery when fresh; margin membranous, thin, broadly sterile to entirely fertile; subiculum thin, less than 0.5 mm. thick; tubes 2-5 mm. long, mouths white when fresh, drying white, yellowish or cinnamon-buff, angular, becoming dentate-lacerate, 2-4 per mm. or longer; dissepiments thin; spores hyaline, smooth, ellipsoid, showing a tendency to co-

here in groups of two, four or more, $3.5-5.5 \times 3-3.5 \mu$; cystidia usually present, usually as fusoid, capitate-incrusted bodies, or entirely incrusted bodies, $3-7 \mu$ in diameter; hyphae somewhat branching, cross walls present, no clamp connection, $3-4 \mu$ in diameter in trama, $3-6 \mu$ in subiculum.

On bark and wood of deciduous trees.

13. *P. vaporaria* (Pers.) Fr.

Fig. 11

Fructification effused, thin, the mycelium creeping into the wood, floccose, white, no sterile margin; subiculum thin and papery; pores rather large, angular, up to 1 mm. long, white, becoming pallid, crowded in a firm persistent stratum; mouths becoming compound and labyrinthiform or dissepi-ments soon breaking up; spores hyaline, smooth, cylindric, $4-5 \times 2.5 \mu$; hyphae hyaline to brownish, clamp connections present, $2-3 \mu$.

On bark and wood of all kinds.

Poria papyracea (Schw.) Cooke is similar to this species but is found on Vitis branches.

14. *P. attenuata* (Peck) Cooke

Fig. 21

Fructification effused for several centimeters on wood or bark, annual, separable, thin (less than 1 mm.); margin very narrow, white, thin, slightly pubescent or nearly glabrous, not fimbriate; subiculum thin, light colored; pores less than 0.5 mm. long in dried specimens; mouths pinkish ochre to light buff, pinkish cinnamon, or light ochraceous salmon when fresh, unchanging or changing to more or less cinnamon when dry, usually glistening, angular or subangular, thin walled, entire, 5-6 per mm.; spores hyaline, smooth, ellipsoidal, $3-4 \times 2-3 \mu$; cystidia very conspicuous, embedded or projecting, hyaline, incrusted, $30-80 \times 4-10 \mu$; hyphae hyaline, simple, $3-4 \mu$ in diameter, no cross walls or clamp connections.

On dead wood and bark of deciduous trees.

This species may be the same as *P. vinctus* Berk.

Lloyd states in Mycological Notes 2:374, 1908, that *Poria europa* Karsten is the same as this species. *Poria nitida* (Pers.) Fr. is probably closely related.

15. *P. salmonicolor* Berk. and Cooke

Fig. 14

Fructification broadly effused, arising from a white mycelium, rich salmon color when fresh, becoming darker, pecan brown to Rood's brown, thin near margin; about 8 cm. long, and 3 cm. wide in our specimen; pores 1-3 mm. long, at first subfleshy, even, medium sized; dissepiments thin, 3-4 per mm., becoming oblique when longer; spores hyaline, smooth, $5.5-8 \times 3-5 \mu$; basidia 4μ in diameter; hyphae hyaline, yellowish in mass, $2-4 \mu$ in diameter, simple to branching.

On charred surfaces of wood. Not common.

16. *P. spissa* (Schw.) Cooke

Fig. 15

Fructification perennial, widely effused, thin, with one layer of tubes, but becoming thick when composed of two or more distinct layers, generally separable in a layer from substratum, margin sterile, compactly tomentose, warm buff to ochraceous buff; subiculum thin but conspicuous even in dried specimens, light colored; tubes 0.5-5 mm. long in each layer; mouths orange buff to ochraceous orange when fresh, dark red or blood red when bruised, orange cinnamon to hazel or seal brown when dry, having a resinous appearance, subrounded, 4-6 per mm., when dry almost invisible; dissepiments entire; spores allantoid, hyaline, $3.5-4.5 \times 1 \mu$; cystidia none; hyphae of subiculum and trama compact, thin-walled, hyaline except for tips which are filled with a brownish substance, branched, $2-4 \mu$ in diameter, often slightly incrustated with small crystals, cross walls present but not conspicuous; clamp connections lacking.

On rotten wood of deciduous and coniferous trees.

This is a very distinctive species and is easily recognized when once known. Overholts describes the species as *Poria laetifica* (Peck) Sacc. from which the above description was adapted. However, Schweinitz's specific name takes precedence over that of Peck, and is so referred to here. The only apparent difference between Overholt's description of *Poria laetifica* Peck and *Poria spissa* (Schw.) or *Polyporus spissus* Fr. is that *laetifera* is annual while *spissa* is perennial. Speci-

mens of both forms are in the State University of Iowa mycological herbarium.

17. *P. nigra* Berk.

Fructification effused, in elongated patches, distinctly black or rich dark brown, hard, rather thick, even, not separable from substratum, margin slightly raised, pubescent, dark brown or black; subiculum hard, 1-5 mm. thick; pores 1-7 mm. long, minute, round, averaging 6-8 per mm., umber within, mouths black; subhymenial layer of a hyaline cellular structure; spores not found; cystidia present but few, brown, small, 15-20 μ long; hyphae dark brown, thick walled, 3-5 μ broad.

On rotten logs.

18. *P. barbaeformis* Berk. and Cke.

"Fungus wholly resupinate, the margin thin, white; the hymenium, fulvous; the pores small elongate with thin dissepiments."

This description was taken from Macbride's paper. There is one specimen in the State University of Iowa herbarium. The specimen, however, is too fragmentary for accurate study.

19. *P. punctata* Fr.

Fig. 18

Fructification effused for several centimeters in elongated patches on wood or bark, adnate, never loosening from substratum, thicker in the center, up to 1.5 cm., becoming thin at the margin with a narrow sterile yellow-brown tomentose border, perennial; subiculum thin, membranous, disappearing; pores 1-2 mm. long each season, separated by a distinct narrow layer of context, mouths minute, hardly discernible to the naked eye, averaging 6-8 per mm., round or subrounded, thick walled, entire, surface of pores yellowish brown, buffy brown or brussels brown (Ridgway); spores hyaline, smooth, globose, or subglobose; basidia inflated, 7-10 μ broad; setae absent, sometimes hyaline; cystidia-like hyphae project from the hymenial surface; hyphae brown, long, slightly branching, septate, 3-4 μ .

On *Ostrya virginiana* and other deciduous trees.

20. *P. obliqua* Pers.

Fructification annual, hard, uneven, thick, pallid becoming chocolate brown, commonly projecting crest at border; subiculum brown, thin, mostly composed of pores; pores long, oblique, minute, 5-6 per mm., angular; spores hyaline, smooth, broadly elliptical $4-4.5 \times 2-2.5 \mu$; cystidia very few, short, pointed, brown, $10-15 \times 5 \mu$; hyphae brown, with cross walls, also a network of hyaline hyphae in subhymenium.

On dead trunks of ironwood (*Ostrya*). Not common.

21. *P. viticola* (Schw.) Cooke

Fig. 17

Fructification often broadly and irregularly effused but frequently in narrow elongated patches, inseparable, annual or persistent, margin narrow, tawny, pubescent or strigose, sometimes disappearing, usually persistent; subiculum very thin, rusty brown; pores 1-2 mm. long, averaging 1-3 per mm., mouths ochraceous brown or tawny olive at first, when dry snuff brown or buffy brown, angular to sinuous or daedaloid, with a finely velutinous surface at first, becoming more glabrous, dissepiments thin, entire; spores hyaline, smooth, cylindrical, $6-7 \times 2-2.5 \mu$; setae abundant, brown, no cross walls or clamp connections, $2-3 \mu$ broad, narrow hyaline, incrustated hyphae present.

On bark and wood of deciduous trees of *Acer*, *Populus*, *Quercus*, *Salix*, *Vitis*, and probably other hosts. The specimens studied were on oak and *Vitis*.

Syn. *Trametes tenuis* Karst.; *P. superficialis* (Schw.) Cooke; *T. setosus* Weir.

22. *P. ferruginosa* (Schrad.) Fr.

Fig. 16

Fructification broadly effused, surface often uneven or undulate, when young with a brown tawny pubescent margin, becoming entirely fertile when mature, closely adhering to substratum, annual or perennial, 0.5-5 mm. thick; subiculum brown, about 0.5 mm. thick; pores 1-2 mm. long in each layer when perennial, brown within or the older layers somewhat whitish pubescent under lens, mouths cinnamon, sayal brown or snuff brown, subrounded or subangular, dissepiments

thin when mature, 4-6 per mm.; spores hyaline, smooth, oblong-ellipsoid or oblong, $4.5-5 \times 2-3 \mu$ (not found in specimens studied); hyphae brown, straight and rigid, no clamp connections, no cross walls, $2-3 \mu$ in diameter, in some specimens narrow incrustated hyaline hyphae project out from hymenial surface of tubes; setae brown, sharp pointed, fairly abundant, projecting $15-30 \mu$ beyond basidia, $5-7 \mu$ in diameter.

On dead and living trees of wood of deciduous trees.

This species differs from *P. viticola* only very slightly. The spores in *viticola* are longer and more slender, measuring $6-7 \times 2 \mu$; in most cases in *P. viticola* the setae are also longer, projecting $25-40 \mu$ and the tubes are occasionally somewhat daedaloid, a condition not found in *P. ferruginosa*.

23. *P. setigera* Peck.

Fig. 98

Fructification effused, tough, thin, adnate, surface rough, margin whitish or cream buff, sterile; subiculum brown, 1-5 mm. thick, much thicker than length of pores; pores very short, less than 0.5 mm., mouths mostly round, drab to wood brown or fuscous, and often with a grayish pruinosity, dissepiments fairly thick, entire, 4-5 per mm.; spores hyaline, smooth, ellipsoid to reniform, $5-6 \times 2-4 \mu$; setae very prominent, pointed, brown, very large in trama and subiculum, and smaller between basidia; hyphae brown, branching, cross walls present, clamp connections absent, $2-4 \mu$ in diameter in trama and subiculum; marginal subiculum with hyaline, branched hyphae, $2-5 \mu$ broad.

On wood of deciduous trees.

24. *P. rufa* Schrad.

Fig. 19

Fructification effused, more or less fleshy, coriaceous, thin, adnate, even, determinate, rufous; pores minute, 2-3 per mm., acute, thin walled when dry; spores hyaline, smooth, ellipsoid, $5.5-7 \times 2.5-3 \mu$; hyphae hyaline to reddish, simple to branched, septate.

On old trunks.

Syn. *P. haematodes* Rost.

The occurrence of this species in Iowa is doubtful. A

specimen in the mycological herbarium has, however, been referred to this species by Macbride.

Genus GLOEOPORUS Mont.

Sporophore coriaceous or fleshy tough, rather thin, flexible, dimidiate, sessile, velvety to glabrous; margin acute; context usually white; hymenophore when fresh consisting of a superficial gelatinous, at first punctiform layer, later with small round pores, pores white, flesh colored or dark brown, purple on drying; spores hyaline, allantoid.

Our only species may be recognized by the soft, white, conchate pileus and the thin gelatinous, partly separable hymenial layer.

Only one species is represented in Iowa.

1. *G. conchoides* Mont.

Pileus coriaceous, pliant, sessile, reflexed, effused-reflexed or rarely resupinate; whitish; light buff or pinkish buff (Ridg.), velvety to glabrous, margin narrowly sterile below; context white, 1-4 mm. thick; hymenophore when fresh or moist, waxy and separating from the context in a thin elastic layer, flesh colored to cocoa brown or darker, pores less than 1 mm. long, circular, small, averaging 5-6 per mm.; spores hyaline, smooth, allantoid, $3-4.5 \times 0.5-1 \mu$; cystidia none; hyphae branched, clamp connections present, 4μ in diameter.

On dead deciduous wood, common on poplar logs and willow.

Syn. *Polyporus dichrous* Fr.; *Polyporus nigra-purpurascens* Schw.

Genus TRAMETES Fries

Sporophore coriaceous, corky, or woody; pileate; sessile, reflexed, effused reflexed or sometimes imbricate; epixylous, annual; hymenium not in a distinct stratum, but the tubes sunken to unequal depths in the context so that their bases do not form a continuous line with the context; pores circular, angular, or irpiciform, sometimes decurrent or sub-decurrent; context white or brown; spores hyaline, smooth; cystidia none.

The species in this genus may easily be confused with species of Lenzites, Daedalea, and Polyporus. From Lenzites and Daedalea they may be distinguished by the less lamellate, and more poroid hymenophore; from Polyporus by the fact that

in that genus the pores form a distinct stratum and are not sunken to unequal depths in the context.

KEY TO SPECIES OF TRAMETES

- a. Context white or whitish -----b
- a. Context tan to light brown, yellowish brown, or rusty brown-----d
 - b. Pileus more than 1 cm. thick-----1. *T. suaveolens*
 - b. Pileus less than 1 cm. thick-----c
- c. Pileus brown; mouths of tubes averaging three or more per mm.-----
 - 2. *T. serialis*
- c. Pileus white or whitish; mouths of tubes averaging 1-2 per mm.; growing on wood of deciduous trees, often on structural timbers.-----
 - 3. *T. sepium*
 - d. Pileus hirsute or hispid; fibrous to corky; usually more than 5 mm. thick; tubes 2-10 mm. long; pores averaging about 1 per mm.-----4. *T. hispida*
 - d. Pileus finely tomentose to glabrous-----e
- e. Context brown, yellowish brown or rusty brown-----f
- e. Context light brown -----g
 - f. Pileus grayish brown to cinnamon-brown; pores 2-3 per mm., dissepiments thin -----See *Lenzites vialis*
 - f. Pileus fulvous to umber-black; dissepiments thick, zonate or sulcate -----5. *T. protracta*
- g. Pileus umber-brown to almost black; context less than 1 mm. thick -----
 - 6. *T. mollis*
- g. Pileus palid to wood-colored; context more than 1 mm. thick-----
 - 7. *T. malicola*

1. *T. suaveolens* Linn. ex Fr.

Sporophore sessile; pileus 3-10 x 5-16 x 1-5 cm., white, whitish, gray or yellowish, villous-tomentose to glabrous, azonate, margin obtuse; context white, or whitish, corky, 0.5-2 cm. or more thick; tubes 0.3-1.5 cm. long, the mouths white to dark colored, averaging 1-3 per mm.; spores cylindrical, 8-12 x 3-4 μ ; cystidia none; hyphae sometimes branched, some of them always 8-12 μ ; on dead or diseased willows.

2. *T. serialis* Fr.

"Sporophore often resupinate; pileus, when present, 0-1 x 1-4 x 0.3-0.8 cm., of a uniform brown color, zonate, nearly glabrous; context white, not more than 1 mm. thick; tubes 2-5 mm. long, the mouths white or whitish, circular to angular, averaging 3 per mm.; spores oblong-elliptic, cylindric-elliptic, or narrowly fusoid, 7-8 x 2-3 μ ; cystidia none; hyphae some-

what branched, 2-4 μ ; on dead wood." The above description is adapted from Overholts (23).

One collection from Iowa by Macbride agrees with Sydow's *Mycothica germanica* No. 2259, a European collection.

3. *T. sepium* Berk.

Fig. 23

Pileus coriaceous, sessile or effused reflexed, usually somewhat imbricate, usually distinctly unguulate, white or whitish, broadly attached behind, azonate to slightly zonate, glabrous or nearly so, 0.3-1 x 0.8-2.5 x 0.2-0.7 cm.; context white, 0.1 cm. or less in thickness; pores 2-5 mm. long, mouths white to pallid, circular, angular, or sinuous, averaging 1-2 per mm.; spores hyaline, smooth, cylindric or cylindric-ellipsoid, 8-9 x 2.5-3 μ ; cystidia none; hyphae branched, 3-5 μ in diameter; on wood of deciduous trees, oak, boxelder, etc.; often on fences, posts, etc.

Syn. "*T. (Poria) flavescens* Schw. resupinate species, probably a form of *T. sepium*." Overholts.

4. *T. hispida* Bagl.

Fig. 24

Pileus corky, sessile, reflexed, often imbricate, surface covered with a dense yellowish or dark brown hirsute or strigose pubescence, 1.5-6 x 1.5-12 x 0.5-2.5 cm.; context light brown, 2-10 mm. thick; pores 2-10 mm. long, mouths grayish-brown or darker, angular, often very uneven, averaging about 1 per mm. or larger; spores hyaline, smooth, cylindric, 11-14 x 3.5-4 μ ; cystidia none; hyphae hyaline or light brown, hyaline ones branched 3-4 μ , brown ones unbranched and wider 3-8 μ ; on willow, poplar and cottonwood trees.

Syn. *T. Peckii* Kalchbrenner; *T. funalis* Fries; *T. trogii* Berk.; *Funalia stuppea* Berk. ex Murrill.

5. *T. protracta* Fr.

Pileus coriaceous to rigid, sessile, surface fulvous to umber-black, sometimes grayish with age, glabrous to rimose with age, margin obtuse, sometimes lighter in color, 2-6 x 3-10 x 0.5-3 cm.; context yellowish brown or rusty brown, 5-15 mm. thick; pores 1-10 mm. long, mouths dark brown, angular, ob-

long, or daedaloid, dissepiments rather thick, averaging about 2 per mm.; spores hyaline, smooth, cylindric, 8-12 x 3.5-5 μ ; cystidia none; hyphae 3-5 μ , some broader.

Usually on dead wood of coniferous trees.

6. *T. mollis* Sommerf. ex Fr.

Sporophore effused-reflexed or entirely resupinate; pileus grayish, umber-brown or darker, zonate, not distinctly pubescent, 0-2.5 x 1-4 x 0.1-0.5 cm.; context light brown, less than 1 mm. thick; tubes subcircular to angular or sinuous, sometimes becoming irpiciform, 2-3 mm. long, mouths grayish to brown, averaging 1-3 per mm.; spores cylindric or cylindric-ellipsoid, 8-10 x 3-4 μ .

On dead wood of deciduous trees.

7. *T. malicola* B. and C.

Fig. 25

Fructification corky to woody, effused-reflexed or resupinate; pileus when present, light brown or wood-colored, azonate or lightly zonate, glabrous or nearly so, 0-1.5 x 1-5 x 0.3-1.5 cm.; context light wood color, 2-5 mm. thick, sometimes thicker; pores 2-7 mm. long, occasionally in layers, same color as context, mouths light brown, circular, angular, or sinuous, averaging 1.5-3 per mm.; spores hyaline, smooth, cylindric, 8-10 x 2-3.5 μ .

On dead wood of deciduous trees.

T. serpens Fr., described by MacBride (20) and in N. A. F. No. 1707, is probably a *Poria*.

Genus *CYCLOMYCES* Kunzle and Fr.

Sporophore coriaceous, membranous, tough, stipitate or sometimes resupinate; orbicular, annual, terrestrial; fuscous or cinnamon-brown; hymenophore at first poroid but soon breaking up into continuous concentric lamellae; dissepiments thin, spores brown, smooth, ovoid.

Cyclomyces has sometimes been referred to the Agaricaceae but is here included in the Polyporaceae because of the marginal pores and more coriaceous texture of the pileus. Only one species is represented in this state and this one very rarely found. It is easily distinguished, however, by its concentrically arranged lamellae.

ate, densely tomentose or velvety, margin thin, 2.5 x 2.9 x 0.3-1 cm.; context white to cream color, 0.5-1.5 mm. thick; hymenophore lamellate, sometimes poroid, lamellae white, tan or light-wood colored, coriaceous, thin, straight, branching or anastomosing, about 1 mm. apart; 0.3-10 mm. broad; spores hyaline, smooth, cylindric or allantoid, 4.5-7 x 1.5-2.5 μ ; cystidia present, hyaline, sharp-pointed or blunt hairs, 24-40 x 4-5 μ ; hyphae simple to branching.

On dead wood of deciduous trees. Common on oak.

2. *L. vialis* Pk.

Fig. 27

Pileus coriaceous or rigid, sessile, effused-reflexed, or occasionally substipitate when growing on top of a log, to resupinate, grayish-brown to cinnamon-brown, glabrous or nearly so, 1.4 x 2.7 x 0.2-0.8 cm.; context brown, 1-5 mm. thick; hymenophore more or less poroid, or daedaloid, less often completely lamellate, brown, averaging 2-3 per mm., 1-4 mm. broad; spores hyaline, smooth, cylindric, 7-9 x 2.5-4 μ ; cystidia none; hyphae brown to hyaline, rarely branched, 2-6 μ .

On wood of deciduous and coniferous trees, and on structural timbers. Often on coniferous bridge planks, etc.

This species approaches very close to *Daedalea*. It is also a very variable species.

Syn. *Trametes pallida-fulva* Berk.; *Lenzites trabea* Pers. ex Fr.

3. *L. saepiaria* Fr.

Fig. 28

Pileus coriaceous to rigid, sessile, effused-reflexed to rarely resupinate, bright yellowish brown to dark brown, zonate, strigose tomentose, 1.5 x 2.7 x 0.3-1 cm.; context yellowish brown or rusty brown, 1-5 mm. thick; hymenophore lamellate, sometimes daedaloid or poroid, the lamellae brown, about 1 mm. apart, 2-5 mm. broad; spores hyaline, smooth, cylindric, 8.5-10 x 2.5-4 μ ; cystidia none; hyphae rarely branched, 4-6 μ .

On dead wood of coniferous trees, rarely deciduous trees.

Syn. *Glocophyllum hirsutum* Schaeff. ex Murrill.

Genus DAEDALEA Pers. ex Fr.

Sporophore coriaceous, corky or somewhat woody; pileate, sessile or effused-reflexed; epixylous; annual or persisting for

two or three years; context white or pallid (never dark brown); trama of context and tubes continuous; hymenium typically labyrinthiform but sometimes varying to poroid, irpiciform or lamellate; spores smooth, hyaline.

KEY TO SPECIES OF DAEDALEA

- a. Pileus densely tomentose to hirsute, thin and coriaceous, flexible; context about 1 mm. thick; hymenium at first labyrinthiform, but soon becoming irpiciform -----1. *D. unicolor*
- a. Pileus velvety or glabrous; rigid, woody or corky; context thicker; hymenium normally labyrinthiform but varying to porose, never irpiciform -----b
 - b. Pores less than 0.5 mm. in transverse section, surface of pileus white or whitish -----2. *D. ambigua*
 - b. Pores one or several mm. in transverse section; surface usually grayish, brownish or discolored-----c
- c. Pileus thick, triangular, margin usually thick; walls of pores obtuse; found on wood of oak and chestnut -----3. *D. quercina*
- c. Pileus thinner, applanate; margin thin; walls of pores not obtuse; found on other hosts -----4. *D. confragosa*

1. *D. unicolor* Bull. ex Fr.

Fig. 29

Pileus coriaceous, tough, flexible, sessile, effused-reflexed, rarely resupinate, whitish, cinereous, yellowish or brownish, villous, strigose or hirsute, zonate, zones often variously colored, margin thin, 0.5-5 x 2-8 x 0.2-0.3 cm.; context white, 1 mm. or less thick; pores 1-4 mm. long, distinctly labyrinthiform at first, and generally remaining so along margin, averaging 2 per mm., later breaking up into teeth, mouths white, cinereous or umber; spores hyaline, smooth, ellipsoid or ovoid, 5-6.5 x 3-3.5 μ ; cystidia none; hyphae usually not branching, 2-4 μ .

On dead wood of deciduous trees. Elm, birch.

2. *D. ambigua* Berk.

Pileus corky or woody, rigid, sessile, sometimes appearing substipitate, thick, convex, azonate, minutely velvety to glabrous, white to umber or darker at the base, 3-14 x 5-20 x 0.3-2.5 cm.; context white, punky to corky, 0.2-1 cm. thick; pores 2-4 mm. long, mouths circular, to linear or daedaloid, mouths white or yellowish, averaging 2-3 per mm., walls thick

and entire; spores not found; cystidia none, branched paraphyses sometimes present; hyphae simple, 3.5-4.5 μ .

On stumps and trunks of deciduous trees.

The species is reported by Macbride.

No specimen from Iowa in the State University of Iowa Herbarium.

3. *D. quercina* Linn. ex Fr.

Pileus rigid, corky or woody, sessile, whitish or pale wood color, umbrinous or almost black, glabrous, azonate or only slightly zonate, margin usually thick and obtuse, perennial, 4-12 x 4-15 x 1.5-6 cm.; context pallid or light brown, corky, 0.2-1 cm. thick; tubes 1-3 cm. long, the mouths whitish to umber, daedaloid or lamellate, 1 mm. or more broad, the walls thick and obtuse; spores cylindric, smooth, hyaline, 5-6 x 2-3 μ ; cystidia none; hyphae simple, 4-6 μ .

On logs or trunks of oak. Not common.

4. *D. confragosa* Bolton ex Fr.

Fig. 30

Pileus corky to woody, rigid, sessile, dimidiate, sometimes zonate, convex, grayish, cinereous or brownish, glabrous to rugose, scabrose, occasionally imbricate, margin thin, entire, 1.5-9 x 2-14 x 0.2-1.5 cm.; context white, becoming darker with age, 0.1-1 cm. thick; pores 1-10 mm. long, mouths circular or elongated to labyrinthiform or lamellate, tan, cinereous, or flesh-colored, variable in size; spores hyaline, smooth, cylindric or allantoid, 5.5-6 x 1.5-2 μ ; cystidia none, paraphyses hyaline or slightly bluish, branched; hyphae simple, 4-8 μ .

On dead wood or living deciduous trees, especially willows.

This fungus takes on many different forms and is thus sometimes confusing. In the young stages the context seems to be thicker, becoming thinner with increased growth.

Syn. *Lenzites crataegi* Berk.; *Lenzites cookeii* Berk.; *Daedalea corrugata* Klotzsch.

Genus FAVOLUS Fr.

Sporophore coriaceous, fleshy-tough when fresh, semi-stipitate, annual, epixylous; context white, thin; hymenium covering angular or hexagonal pores, often radiating outward from the stipe; stipe typically lateral; spores hyaline.

Polyporus arcularius may be separated from *Favolus* by the centrally placed and usually longer stipe.

KEY TO SPECIES OF FAVOLUS

- a. Pores rather large, 0.5-1 mm., sometimes larger, hyphae 3-4 μ -----
 ----- *F. canadensis*
 a. Pores smaller, 2-3 per mm.; hyphae 5-9 μ ----- *F. rhipidium*
 This key was taken from Overholts.

1. *F. canadensis* Klotzsch

Pileus fleshy-tough, thin, reniform, to orbicular, generally laterally or excentrically stipitate, stipe very short if present; surface very finely squamulose or innately fibrillose, ranging in color from reddish-brown to cream color or white, becoming glabrous, 1-4 x 1-8 x 0.1-0.7 cm.; context white, 0.5-2 mm. thick; pores 1-5 mm. long, mouths white to yellowish, angular, hexagonal, longer in the radial direction, 0.5-3 mm. long x 0.5-1 mm. broad; spores hyaline, smooth, cylindric, 9-11 x 3-4 μ ; cystidia none; hyphae branched, 3-4 μ .

On dead deciduous trees.

Syn. *F. europaeus* Fr.; *F. microporus* Murrill; *F. ohioensis* Berk. and Mont.; *F. striatulus* Ellis and Ev.; *Hexagona alveolaris* Murrill.

2. *F. rhipidium* Berk.

Pileus coriaceous, reniform, stipitate, stipe more prominent, lateral, pruinose, 0.5-2.5 cm. long, 1-4 mm. thick; surface alutaceous to white, finely squamulose; context white, 1 mm. or less thick; pores 1-2 mm. long, mouths white, denticulate, averaging 2-3 per mm. transversely and about 2 per mm. longitudinally; cystidia none or of a few projecting hyaline hairs, 2-3 μ broad; hyphae 5-9 μ in diameter.

On dead wood of deciduous trees.

Macbride reports having seen a single specimen which agreed with this description. "It occurs in little dense caespitose tufts." This specimen, said to be seen by him, was 2 cm. in each dimension, with a stipe about 6 mm. long. A number of specimens in the State University Herbarium agree with this description.

GENUS GANODERMA Karst.

Sporophore corky to woody, sessile or stipitate, perennial or annual, epixylous, surface sulcate, covered with a reddish

brown varnish or crust-like surface; context punky, brown or brownish; tubes cylindric, concolorous with context; spores yellowish or brown, ovoid.

KEY TO SPECIES OF GANODERMA

- a. Spores echinulate, sporophore perennial, pileus and stem at first red-varnished, the varnish disappearing and the pileus becoming whitish or yellowish when mature -----1. *G. Curtisii*
- a. Spores smooth, sporophore annual, pileus and stem strongly red-varnished, the varnish not disappearing -----2. *G. sessile*

1. *G. Curtisii* Berk.

Fig. 31

Pileus corky, stipitate, reniform or flabelliform, convex above, concave below, surface glabrous, covered with a thin crust of red varnish at least in part, zonate, margin usually truncate or obtuse, entire, 3-12 x 3-20 x 1-2 cm.; context corky, light colored above, brown and firm next to the tubes, 5-10 mm. thick; pores 3-12 mm. long, the mouths white, yellow or brownish, averaging 3-5 per mm.; stipe lateral with color and context like the pileus, 2-10 mm. long, 5-20 mm. thick; spores ovoid with a truncate base, echinulate, yellowish brown, 9-11 x 5-7 μ ; cystidia none; hyphae hyaline or brown, somewhat branched, 3-5 μ .

On stumps and trunks of deciduous trees.

2. *G. sessile* Murrill

Fig. 32

Pileus coriaceous, corky or fibrous, tough, sessile or stipitate, surface covered with a thin reddish or chestnut colored crust, polished, shining, glabrous, sulcate-rugose, zonate, 3-12 x 3.5-20 x 0.5-3 cm.; context made up of an upper light colored and lower brown layer, never entirely white, 2-15 mm. thick, thicker at base; pores 0.3-1.5 cm. long, mouths white to umber or tan, averaging 3-5 per mm.; stipe when present central, lateral or excentric, color and context like pileus, 0-10 cm. long, 0.5-1 cm. thick; spores light brown, slightly roughened or perforated, 9.5-12 x 6-8 μ ; cystidia none; hyphae hyaline or brown, branched, 4-10 μ .

On stumps and trunks of deciduous trees, especially oak.

Syn. *Polyporus lucidus* (Leyss.) Fries; *Ganoderma subperforatum* Atkinson; *Fomes lucidus* Leyss. ex Cooke.

Genus FOMES Fr.

Sporophore woody or corky from the beginning, seldom soft or watery; sessile, applanate or ungulate, epixylous, perennial, forming a new stratum of tubes each year or more often; context soft and punky to hard and woody, white, reddish or brownish; pileus sometimes incrustated, often rimose; hymenophore poroid, dissepiments usually thick; spores hyaline or brown; setae present or absent.

KEY TO SPECIES OF FOMES

- a. Context white, flesh colored, wood-colored, or rose-colored; spores always hyaline; setae never present -----b
- a. Context yellowish brown or dark brown; spores hyaline or brown; setae present or absent -----h
 - b. Context flesh colored, pinkish or rose colored; light brown when dried -----c
 - b. Context white or yellowish -----d
- c. Pilei usually growing on wood of deciduous trees, especially on ash; tubes 3-5 mm. long each season; spores subglobose, 6-7 x 5-6 μ ; hyphae of context 6-9 μ in diameter ----- 1. *F. fraxineus*
- c. Pilei usually growing on wood of coniferous trees; tubes 1-2 mm. long each season; spores cylindric or slightly allantoid, 6-10 x 2-4 μ ; hyphae of context 4-5 μ in diameter ----- 2. *F. roseus*
 - d. Sporophore small, scarcely more than 2 cm. broad and 1 cm. thick -----e
 - d. Sporophore larger -----f
- e. Pileus usually scutellate, uniformly black even when young; growing on limbs of alder, and witch-hazel; spores cylindric, 8-9 x 2.5-3.5 μ ; hyphae of context much branched ----- 4. *F. scutellatus*
- e. Pileus ungulate, becoming black only at the base; zonate and concentrically sulcate with age; growing on structural timbers, and deciduous trees; spores ovoid, with truncate base, 10-12 x 6-7 μ ; hyphae unbranched or nearly so ----- 3. *F. ohieni.*
 - f. Pileus even, rarely rimose, surface concolorous with the context; layers of tubes separated by a distinct layer of context; growing on maple ----- 5. *F. connatus*
 - f. Pileus rimose or slightly incrustated, surface of pileus darker than context; layers of tubes not separated by a layer of context; growing on other trees -----g
- g. Pileus applanate, not more than 2 cm. thick; crust brown to black; spores subglobose, 4-5 μ ; hyphae of context 4-8 μ in diameter ----- 6. *F. annosus*
- g. Pileus convex to ungulate, more than 2 cm. thick; surface gray to black; mouths of tubes 2-3 per mm; growing mostly on ash ----- 7. *F. fraxinophilus*

- h. Setae absent, spores hyaline ----- i
- h. Setae present, spores hyaline ----- k
- i. Pileus strongly incrustated; growing on living trees; spores cylindric elliptic, 12-16 x 4-5 μ ; context punky, the hyphae 5-10 μ in diameter ----- 8. *F. fomentarius*
- i. Pileus not incrustated; spores subglobose, 4-6 μ ; context woody ---- j
 - j. Context fulvous, opaque; tubes in older layers generally conspicuously white-stuffed; hyphae of context 3-4 μ in diameter ----- 9. *F. igniarius*
 - j. Context honey-colored, lustrous; tubes in the older layers not white-stuffed; hyphae of context 4-6 μ in diameter ----- 10. *F. Bakeri*
- k. Sporophore growing on coniferous trees or the wood of same; tubes not white stuffed or incrustated ----- 11. *F. pini*
- k. Sporophore not growing on coniferous trees or wood ----- l
 - l. Pileus thin and conchate, usually partly or entirely resupinate; growing on old logs or rarely on living trees; spores subglobose, 4-6 μ ----- 12. *F. conchatus*
 - l. Pileus not thin and conchate, sometimes ungulate, growing on trunks and branches of trees ----- m
- m. Sporophore growing on *Prunus*; tubes in the older layers not white-stuffed or incrustated, spores subglobose, 4-6 μ ----- 13. *F. fulvus*
- m. Sporophore growing on other trees ----- n
 - n. Sporophore growing on oaks, birches, etc.; tubes in older layers white-stuffed or incrustated; spores subglobose, 4-6 μ ----- 9. *F. igniarius*
 - n. Sporophores not as above, may be growing on above-mentioned hosts, however ----- o
- o. Setae present; spores brown, ellipsoid to globose, 3-3.5 x 4-4.5 μ ; tubes long, over 5 mm. each season; growing on oak ----- 14. *F. everhartii*
- o. Setae absent; spores brown ----- p
 - p. Sporophore growing on locust trees (*Robinia*); pileus unincrustated, soon rimose; context woody; spores globose, smooth, 4-5 μ ----- 15. *F. rimosus*
 - p. Sporophore usually growing on logs and stumps, sometimes on living trees other than locust; pileus incrustated, never rimose; context punky to soft corky; spores slightly echinulate, ovoid with a truncate base 4-5 x 5-7 μ ----- q
- q. Crust of pileus easily indented; perennial by the addition of a second year's growth of pileus below the first ----- 16. *F. lobatus*
- q. Crust of pileus hard and horny; truly perennial ----- 17. *F. applanatus*

1. *F. fraxineus* Bull. ex Cooke

Pileus applanate, plane, or convex, surface usually light colored with reddish or reddish brown stains or altogether reddish, becoming brown with age, incrustated with a thin hard crust, somewhat zonate, 4-10 x 6-16 x 1-6 cm.; context at first

punky or corky, then hard, 0.4-3 cm. thick, somewhat flesh-colored, often fading out in drying; tubes 2-10 mm. long, often in a single layer, the mouths whitish, pallid, or flesh-colored, averaging 4-6 per mm.; spores subglobose, 5-6 x 6-7 μ ; setae none; hyphae 6-9 μ .

Usually on stumps or trunks of ash trees. Rare.

The above description is adapted from Overholts (34).

This species, reported by Fennell and Overholts, does not seem to be contained in the State University of Iowa Herbarium.

2. *F. roseus* Alb. and Schw. ex Cooke

Pileus unguulate, brownish pink, flesh-colored or pinkish red, often black with age, not incrustated, sometimes sulcate, furrowed on the margin, 2-7 x 2-6 x 2-3 cm.; context pinkish or rose-colored, soft corky or hard, 2-10 mm. thick; tubes 1-3 mm. long, in distinct layers, the mouths pinkish or rosy, averaging 3-5 per mm.; spores hyaline, smooth, oblong-cylindric, 7-10 x 2-4 μ ; cystidia none; hyphae 4-5 μ .

Usually on wood of coniferous trees. Rare.

The above description is adapted from Overholts (34).

Overholts, Fennell and Wilson report this species. It was not studied since there seems to be no specimen in the State University of Iowa Herbarium.

3. *F. ohioensis* Berk. ex Murrill

Fig. 33

Pileus convex to unguulate, dimidiate, sometimes circular and attached by the vertex, pure white at the margin but otherwise brown or black, glabrous and often zonate or sulcate, 0.5-2.5 x 0.5-3 x 0.2-1 cm.; context pallid, indistinctly zonate, 1-3 mm. thick, woody or corky; tubes 1-4 mm. long each season, the mouths chalky-white becoming creameous, 4-5 per mm., circular; spores hyaline, globose, smooth, 5 μ ; conidia ovoid with a truncate base, hyaline, smooth, 10-13 x 6-8 μ ; cystidia none; hyphae simple 3-4 μ in diameter.

On linden, other dead woods, and structural timbers.

Spores described by Murrill (as cited above) were not seen in the specimen studied.

Syn. *Trametes ohioensis* Berk.

4. *F. scutellatus* (Schw.) Cooke

Pileus usually scutellate, rarely dimidiate, small, concave below, surface dark brown or black at least when mature, slightly sulcate, 0.5-1.5 x 0.5-2 x 0.1-0.5 cm.; context isabelline, 2-3 mm. thick, corky to woody; tubes 1-2 mm. long each season, mouths chalky white or pallid, averaging 4-5 per mm., circular or subcircular; spores hyaline, smooth, cylindric, 8-9 x 2.5-3.5 μ ; cystidia none; hyphae much branched, 2-4 μ in diameter; basidia 6-9 μ broad.

Usually on alder and witch-hazel and other soft wood branches, lying on the ground.

Spores were not found in any of our collections.

Syn. *Trametes scutellata* Schw.

5. *F. connatus* Weïnmann ex Gillet

Pileus usually imbricate, dimidiate, convex, white to yellowish, yellow or grayish black in old specimens, glabrous, never rimose, rarely sulcate, 2-10 x 3-15 x 0.5-4 cm.; context 0.3-1 cm. thick, white, soft and corky or hard; tubes 1-5 mm. long each season, very distinctly stratified, with a narrow layer of context between the annual layers, mouths yellowish, darker than context, often glistening, minute, averaging 4-5 per mm.; spores hyaline, smooth, ellipsoid to globose, 3-4 x 4.5-5 μ or 3-4 μ broad; cystidia none; hyaline crystalline bodies present (referred to as cystidia by Lloyd); hyphae 2-4 μ .

No specimen from Iowa seems to be present in the State University mycology herbarium. The specimen studied was from Michigan.

Syn. *F. populinus* (Schum.) Cooke.

6. *F. annosus* Fr. ex Cooke

Pileus applanate or subresupinate, woody, usually thin, irregular gray-brown or uniform light brown, darker with age, sometimes slightly incrustated, zonate, 5-12 x 7-12 x 0.5-2 cm.; context whitish, less than 1 cm. thick, corky; tubes 2-6 mm. long, often in a single layer, mouths yellowish, round or elongated, about 3 per mm.; spores hyaline, smooth, subglobose or ellipsoid, 4.5-5 μ ; cystidia none; hyphae 4-8 μ .

On coniferous trees and stumps.

Reported from Iowa by Overholts and Fennell. Apparently

no specimen in the State University of Iowa Herbarium.

This description was adapted from Overholts.

7. *F. fraxinophilus* Peck

Fig. 34

Pileus convex to unguulate, broad at the point of attachment, surface at first white, becoming grayish black to black, hard and rimose with age, or sulcate, 2-25 x 3.5-40 x 1.5-10 cm.; context cinnamon, thick, woody, 0.5-1.5 cm.; tubes 2-4 mm. long each season, indistinctly stratified, mouths white or brownish, averaging 2-3 per mm., edges obtuse; spores hyaline, smooth, ellipsoid or ovoid, 4.5-6.5 x 6-7 μ ; cystidia none; hyphae 3-5 μ .

Common on trunks of living and dead *Fraxinus*.

Fomes ulmarius reported by Macbride seems to be the same as *F. fraxinophilus*.

8. *F. fomentarius* Linn. ex Gillet

Pileus convex to unguulate, with a smooth, horny grayish crust, zonate or sulcate, 3-15 x 6-20 x 2-15 cm.; context dark brown, 0.3-3 cm. thick, punky or soft corky; tubes 0.5-2.5 cm. long, mouths grey to brown, with a distinct pruinose covering, averaging 3 per mm.; spores hyaline, smooth, cylindric-elliptic 12-16 x 4-5 μ ; setae none; hyphae 5-10 μ .

Common on living wood of deciduous trees, especially on *Betula*.

This species is related to *F. applanatus*, but distinguished from it by the thicker crust, hoof-shaped pileus, and longer tubes.

9. *F. igniarius* Linn. ex Gillet

Fig. 35

Pileus convex or unguulate, first brown then grayish-black or black, surface rimose with age, not incrustated, 3-10 x 5-20 x 2-10 cm.; context brown, ferruginous, zonate, 0.5-3 cm. thick, hard and woody; tubes 2-5 mm. long each season, minute, subhymenial layer hyaline, cellular, mouths brown, averaging 4-5 per mm.; spores hyaline, smooth, globose or subglobose, 4-4.5 x 5.5 μ ; setae present, often scarce, sharp pointed, swollen at base, brown, 16-25 x 6-8 μ ; hyphae brown, 3-4 μ .

On trunks of living deciduous trees.

Fomes nigricans Fr. is a form of *F. igniarius*. The pileus is not roughly rimose, as in *F. igniarius*, but is hard and often found cracking in both directions.

10. *F. Bakeri* Murrill ex Saccardo

Fig. 36

Pileus convex to compressed-ungulate, surface grayish black or blackish on upper surface in our specimens, smooth, not incrustated, 2-3 times sulcate in older specimens; margin brown, rounded or obtuse, 3-8 x 5-14 x 2-5 cm.; context brown, somewhat shining, 1-2.5 cm. thick, woody; tubes 3-5 mm. long each season, mouths brown, circular, averaging 4-6 per mm.; spores hyaline, or in our specimens distinctly yellowish with a prominent greenish guttule when fresh, smooth, globose to subglobose 5-8 μ (5-6 μ in Overholts); setae or cystidia none; hyphae brown, 2-6 μ .

On trunks of living or dead birch trees.

Syn. *F. robustus* Kalch.

Lloyd believes this to be a form of *F. robustus*, without the black rimose crust of the type.

11. *F. pini* Thore ex Lloyd

Pileus unguulate, surface dark brown, rough tomentose, with concentric raised zones, becoming blackish and glabrous, 6-15 x 4-20 x 1-15 cm.; context tawny or ochraceous-tawny, woody, not more than 5 mm. thick; tubes 2-6 mm. long each season, the mouths ochraceous-brown, large, round, elongated, or sometimes daedaloid, 1-3 per mm.; spores hyaline, or brown, smooth, globose, 4-5 μ ; setae present, sharp pointed, projecting 20-30 μ ; hyphae 3-5 μ .

On wood of coniferous trees, both living and dead.

This species is reported as *Trametes pini* by Macbride. Lloyd however found it to be a distinctly perennial species. The specimen reported by Macbride from Iowa was found on pines in Muscatine County. The annual form is referred to as *Trametes abietinus* by Lloyd.

12. *F. conchatus* Pers. ex Gillet

Fig. 37

Pileus sessile, reflexed, effused-reflexed, sometimes mostly resupinate when sessile, thin and conchate, surface dark brown,

grayish brown or almost black, closely concentrically sulcate, roughened, not rimose or incrustated, margin acute, 0.7 x 4-12 x 0.2-3.5 cm.; context light brown, 1.5-3 mm. thick, woody; tubes 1-2 mm. long each season, apparently separated by a layer of context, mouths minute, concolorous or fulvous to dark brown, averaging 4-5 per mm.; spores hyaline, smooth, subglobose, 4-5 μ ; setae present and numerous, sharp pointed, 20-40 x 5-9 μ ; hyphae 2-3 μ .

On dead wood or occasionally on living deciduous trees. Common on *Crataegus* and wild grape.

13. *F. fulvus* Scopoli ex Gillet

Fig. 38

Pileus convex, usually attached by the vertex and subcircular or elongated in form with both margins reflexed or effused-reflexed, rarely strictly sessile, usually dull gray or blackish behind, brown on margin, hardly rimose, somewhat incrustated, 1-4 x 3-8 x 0.5-2.5 or larger in one of our specimens; context brown, woody, 3-8 mm. thick; tubes 1-4 mm. long each season, not at all or not conspicuously white-stuffed in the older layers, mouths round, minute, brown, averaging 4-5 per mm.; spores hyaline, smooth, globose, 3-4 x 4-6 μ ; setae present, sharp pointed, 16-25 x 6-8 μ ; hyphae 3-4 μ .

Common on diseased trunks, stumps, and branches of various species of *Prunus*.

Sny. *Fomes pomaceus* Pers.

C. G. Lloyd uses the name of *F. pomaceus* Pers. instead of *F. fulvus*. Fries, Schroeter, Berkeley, and others held it to be a variety or the same as *Fomes igniarius*.

14. *F. Everhartii* Ellis and Gallister ex von Schvenk

Fig. 40

Pileus convex, rarely unguulate, at first brown, becoming grayish or blackish on upper surface, not incrustated, sulcate, rough and rimose with age, margin remaining brown and velvety, 2.5-11 x 4-20 x 2-15 cm.; context rusty brown, 1-5 cm. thick, woody; tubes 3-6 mm. long each season, mouths brown, changing color when turned in the light, not decurrent but separate by a definite margin, averaging 4-5 per mm.; spores brown, smooth, ellipsoid to globose, 4-5 x 3-4 μ ; setae present,

and numerous, sharp pointed, brown, 2-30 x 7-8 μ ; hyphae brown, 3-6 μ .

Mostly on living *Quercus* trunks.

15. *F. rimosus* Berk.

Fig. 93

Pileus convex to ungulate, surface at first uniformly brown, becoming black, sulcate and rimose with age, no distinct crust, 3-20 x 6-30 x 1.5-10 cm.; context yellowish brown, 0.5-3 cm. thick, woody; tubes 1-4 mm. long each season, mouths minute, brown, averaging 5-6 per mm.; spores brown, globose, 4-5 μ ; setae none; hyphae deep bright yellowish brown, 3-4 μ .

On living trunks of locust trees.

Syn. *Fomes robiniae* Murrill; *Pyropolyporus robiniae* Murrill.

16. *F. lobatus* Schw. ex Cooke

Fig. 41

Pileus plane or depressed, yellowish brown, umber, or rusty brown, thin distinct crust, easily indented, pilei produced for two or three years coming out from below those of the preceding year, sometimes appearing substipitate, margin obtuse, 4-12 x 4-15 x 1-3 cm.; context brown, 0.3-3 cm. thick, soft and punky, harder toward the surface; tubes 1-10 mm. long each season, not white incrustated in the older layers, mouths white, yellowish to brown, darker when bruised, averaging 3-4 per mm.; spores pale brown, minutely echinulate, ovoid, 8-10 x 5.5-7 μ ; setae none; hyphae 2-6.5 μ broad.

Growing on old logs and stumps, sometimes on living trees.

Syn. *Polyporus lobatus* Schw.; *Polyporus reniformis* Morgan.

17. *F. applanatus* Pers. ex Wallroth

Fig. 39

Pileus plane or convex, applanate, or substipitate, usually gray to grayish black, covered with a thick, rigid but fragile, horny crust, indistinctly zonate and sulcate, glabrous, 3-30 x 5-50 x 1.5-7 cm.; context brown, 0.5-5 cm. thick, punky to corky or fibrous; tubes 4-12 mm. long each season, rather distinctly stratified, mouths white, yellowish or umber, becoming darker when bruised, averaging 4-6 per mm.; spores brownish, smooth or slightly echinulate, ovoid with a truncate base, 5-8 x 4-5 μ ; cystidia none, hyphae 2-6 μ .

On logs and stumps, also live trunks of deciduous trees (rarely conifers).

Syn. *Fomes leucophaeus* Mont.; *Elfvigia megaloma* (Lev.) Murrill; *Polyporus leucophaeus* Mont.

Genus POLYSTICTUS Fr.

Sporophore thin, membranaceous or coriaceous, sessile, reflexed, effused-reflexed, stipitate, substipitate or imbricate, epixylous; context 3 mm. or less thick; pores at first superficial punctiform, then becoming deeper; and finally breaking up into teeth, developing from the center or place of attachment toward the margin of the pileus; spores hyaline, smooth.

KEY TO SPECIES OF POLYSTICTUS

- a. Normally with a central stipe-----b
- a. Not stipitate or only substipitate -----c
 - b. Surface of pileus shining cinnamon with silky striations, slightly depressed, the margin often fimbriate or pseudociliate -----1. *P. cinnamomeus*
 - b. Surface of pileus not shining, dull rusty cinnamon to hoary, velvety to glabrous, deeply depressed, margin thicker, less fimbriate -----2. *P. perennis*
- c. Fructification arising from a cup-shaped, sterile body that may disappear or remain for some time near the base on the mature fructification, pileus white or becoming grayish or brownish, found on dead elm branches -----3. *P. conchifer*
- c. Fructification not as above -----d
 - d. Pileus fibrillose-tomentose or glabrous, 1-5 cm. broad, tubes 2-5 mm. long, mouths 1-2 per mm., soon breaking up into teeth -----4. *P. bififormis*
 - d. Pileus velvety to hirsute or tomentose -----e
- e. Context more than 1 mm. thick -----f
- e. Context 1 mm. or less in thickness -----g
 - f. Context 1-3 mm. thick, pileus minutely velvety or shortly villous, conspicuously zonate, with zones of different colors -----5. *P. zonatus*
 - f. Context 1-6 mm. thick, dissepiments thick and entire, zonate but not of different colored zones -----*Polyporus hirsutus*
- g. Pileus multizonate, zones variously colored -----6. *P. versicolor*
- g. Pileus sometimes zonate, but not with multicolored zones -----h
 - h. Hymenophore or layer of tubes often violet-tinted, pileus 1-7 cm. broad, cystidia when present not incrustated except sometimes when capitate at the apex -----7. *P. pargamensis*
 - h. Hymenophore always white, narrowly reflexed, never more than 1 cm. and sometimes entirely resupinate; early becoming irpiciform -----*Polyporus tulipiferus*

1. *P. cinnamomeus* Sacc.

Fig. 72

Pileus thin coriaceous, stipitate, orbicular, convex, umbilicate or depressed in the center, surface bright-cinnamon cinereous, brown or ferruginous, shining, strigose, striate, zonate, margin slightly lobed or undulate, sometimes sterile below, 1-3.5 cm. broad, 1-3 mm. thick; context rusty brown, less than 1 mm. thick; tubes not over 2 mm. long, slightly decurrent, mouths ferruginous or cinnamon, angular, rather large, averaging 2-4 per mm.; stipe central, slightly branching, reddish brown, velvety to villous, 1-4 cm. long, 1-4 mm. thick; spores pale yellow brown, smooth, oblong or ovoid, 6-8 x 4-6 μ ; cystidia none; hyphae simple, brown, 6-9 μ .

On mossy soil or decayed wood, almost reduced to humus, or on clay banks, usually among mosses.

Syn. *Polyporus subsericeus* Peck; *Polyporus oblectans* Berk.; *Polyporus parvulus* Klotzsch; *Polyporus cinnamomeus* Jacq. ex Fries.

2. *P. perennis* Karst.

Fig. 73

Pileus thin and coriaceous, stipitate, circular, infundibuliform, convex to umbilicate, surface brown to cinnamon or cinereous, finely tomentose, substriate, zonate, margin very thin, entire to lacerate, 1.5-6 cm. broad, 1-3 mm. thick; context brown, less than 1 mm. thick; tubes 1-2.5 mm. long, mouths whitish when young, soon brown to cinnamon, angular, averaging 2-4 per mm.; spores hyaline of pale yellowish-brown, smooth, ovoid, 7-8 x 5 μ ; setae none; hyphae simple, brown or yellowish-brown under the microscope.

On dry exposed soil in woods, especially on burned-over earth.

Syn. *Polyporus proliferus* Lloyd; *Coltricia perennis* (L.) Murrill; *Polyporus perennis* Linn. ex Fries.

3. *P. conchifer* Schw.

Fig. 42

Pileus coriaceous, very thin, sessile or attached by a lateral tubercle and appearing substipitate, concentrically sulcate, white, yellowish or grayish, glabrous, sometimes zonate, bearing at the base of pileus a small cup-shaped sterile structure,

1-3 x 1-4 x 0.1-0.3 cm.; context white, less than 1 mm. thick; tubes 2 mm. or less long, mouths white or yellowish, angular, thin walled, dentate, averaging 3 per mm.; spores hyaline, smooth, cylindric or allantoid, 6-7 x 1.5-2 μ ; cystidia none; hyphae 2-4 μ .

On dead branches of deciduous trees, especially elm branches.

Syn. *Poronidulus conchifer* (Schw.) Murrill.

4. *P. biformis* Klotzsch

Pileus coriaceous, soft and pliant when fresh, tough, sessile or effused-reflexed, white to alutaceous, subzonate, with innate radiating fibers, giving it a rough appearance, 1-5 x 1.5-6 x 0.2-0.5 cm.; context white, 1-2 mm. thick; tubes 2-5 mm. long, mouths white to yellowish, circular, angular, dentate and lacerate, usually breaking up into teeth at an early stage, averaging 1-2 per mm.; spores hyaline, smooth, oblong, allantoid, 7-8 x 2-2.5 μ ; cystidia none; hyphae simple, 3-4 μ .

On dead wood of deciduous trees.

5. *P. zonatus* Fr.

Fig. 45

Pileus coriaceous to woody, sessile or effused-reflexed, cinereous, gray or ochraceous, minutely velvety or short villous, concentrically zonate, margin whitish, even, thin, 1-3 x 1.5-5 x 0.2-0.4 cm.; context white 1-3 mm. thick; tubes 1-2.5 mm. long, mouths white or yellowish, circular to angular, obtuse, 3-4 per mm.; spores hyaline, smooth, cylindric, 6-8 x 2-3 μ ; cystidia none; hyphae simple, 5-8 μ .

On dead trunks and branches.

This species is very close to *P. versicolor* except that the context is slightly thicker, and the pores are larger. The spores also seem to be slightly larger in this species.

6. *P. versicolor* Linn. ex Fr.

Fig. 43

Pileus coriaceous, sessile, effused-reflexed, or rosetted, thin, rigid, dimidiate, depressed behind, variable in color and marked by many narrow multicolored zones ranging from white to yellow brownish, reddish, greenish, and blackish, villous or tomentose, shining, often alternating glabrous and tomentose

zones, margin acute, wavy, rounded or lobed, 2.5 x 2.7 x 0.1-0.3 cm.; context white, less than 1 mm. thick, or thicker at the base, 7-8 mm.; tubes 1-2 mm. long, mouths minute, white, yellowish or brownish, round, walls thin, nearly entire, sometimes lacerate with age 3-5 per mm.; spores hyaline, smooth, oblong or allantoid, 5-6 x 1-2 μ ; cystidia none; hyphae simple, 2-10 μ .

On all kinds of dead wood.

One of our most common Polypores. It is easily recognized by its coriaceous rigid substance and by its shining zones of many colors.

7. *P. pargamenus* Fr.

Fig. 44

Pileus coriaceous, membranaceous, pliable, sessile, reflexed, dimidiate or imbricate, often narrowed at the base, whitish, cinereous or brownish with age, villous or velvety pubescent, zonate or azonate, 1-7 x 1-7 x 0.1-0.4 cm.; context white, less than 1 mm. thick; tubes 1-3 mm. long, mouths usually violaceous to white or bay, at first small, irregularly dentate, soon irpiciform, 2-3 per mm. in poroid forms; spores hyaline, smooth, cylindric, allantoid, 5-6.5 x 1.5-2.5 μ ; cystidia present or inconspicuous as projecting capped hyphae, 4-5 μ broad, projecting 5-15 μ ; hyphae simple, 4-6 μ .

On dead wood of deciduous trees.

Syn. *Polyporus pargamenus* Fr.; *Polyporus pseudopargamenus* Thum.; *Coriolus prolificans* Fr. ex Murrill; *Coriolus pargamenus* Fr. ex Murrill.

Genus POLYPORUS Mich. ex Fr.

Sporophore fleshy tough, coriaceous, corky or woody in texture; sessile, effused, effused-reflexed, applanate, or stipitate, sometimes imbricate; hymenophore poroid in a well marked stratum; pores cylindric, angular, sinuous, or sometimes when becoming old breaking up into teeth; context white, yellow, red or brown; pileus variously colored, glabrous, hirsute or pubescent; hispid or waxy, zonate or azonate; epixylous or terrestrial, annual; spores hyaline or colored.

Polyporus comprises a large number of species, varying in structure and texture. It contains no typical resupinate forms.

KEY TO SPECIES OF POLYPORUS

- a. Context white, whitish, pallid or yellow; spores hyaline -----b
- a. Context yellowish red, reddish, brown or brownish; spores hyaline or brown -----uu
 - b. Sporophore stipitate or substipitate -----c
 - b. Sporophore sessile or effused-reflexed -----v
- c. Sporophore consisting of a few or many fleshy pilei arising from a common base, tubercle, or compound, branching stipe; of large size, growing on wood or roots of trees -----d
- c. Sporophore consisting generally of a single pileus, stipe simple or not branching more than once -----j
 - d. Pilei regular in outline and centrally attached, branches of the stipe regular and cylindric in form; spores cylindric.-----1. *P. umbellatus*
 - d. Pilei not regular in outline, stipe not centrally attached -----e
- e. Hymenium some shade of orange or yellow -----f
- e. Hymenium not orange or yellow -----g
 - f. Sporophore bright-sulphur yellow, growing on stumps and trunks of various trees -----2. *P. sulphureus*
 - f. Sporophore orange, expanded on all sides from a radial tubercle, tubes golden yellow, short, mouths becoming brownish, growing on the ground -----3. *P. heteroclitus*
- g. Spores echinulate -----4. *P. Berkeleyi*
- g. Spores smooth -----h
 - h. Surface of pileus white or pallid -----*P. sulphureus* var. *albolabyrinthiformis*
 - h. Surface of pileus not white, usually gray -----i
- i. Pileus fleshy, many pilei arising from a common stalk, pilei always laterally attached, stipe branches irregular -----5. *P. frondosus*
- i. Pileus tough, corkey or leathery, caespitose, surface pallid or light brown, hymenium usually turning black where bruised or on drying -----6. *P. giganteus*
 - j. Sporophore small, not more than 1 cm. high, on oak and chestnut wood -----7. *P. pocula*
 - j. Sporophore always much larger -----k
- k. Context duplex, soft and spongy above, firm next to the hymenium; often much distorted and porous over most of the surface, cystidia present -----8. *P. distortus*
- k. Context not duplex, pores covering only underside of pilei -----l
 - l. Stipe black at the base -----m
 - l. Stipe not black at the base -----q
- m. Sporophore growing in the ground; spores very large, 12-15 x 5-8 μ ; pileus some shade of brown -----9. *P. radicans*
- m. Sporophore growing on wood -----n
 - n. Surface of the pileus brown, smooth, slightly streaked with fine, lighter colored radiating lines -----10. *P. varius*

- n. Pileus without fine lighter colored radiating lines on surface -----o
- o. Pores large, 1-2.5 mm. broad, surface of pileus with distinct squamules -----11. *P. squamosus*
- o. Pores small or medium sized -----p
- p. Pileus tan colored or ochraceous; 2-5 cm. broad; pores averaging 4-5 per mm. -----12. *P. elegans*
- p. Pileus bay or ochraceous, 4-20 cm. broad; pores averaging 5-7 per mm. -----13. *P. picipes*
- q. Sporophore arising from a cup-shaped sterile body that may disappear; pileus white or grayish white when old; found on dead branches of elm -----*Polystictus conchifer*
- q. Sporophore not arising from a cup-shaped sterile body; rarely found on elm branches -----r
- r. Margin of pileus projecting 5 mm. or more beyond the hymenium; hymenium separating smoothly from the context in fresh specimens, growing only on birch -----14. *P. betulinus*
- r. Sporophore not as above -----s
- s. Pileus more or less imbricate, and attenuate to a stem-like base, context hard and firm when dry -----15. *P. osseus*
- s. Context not hard and bony when dry -----t
- t. Pileus bright sulphur yellow -----2. *P. sulphureus*
- t. Pileus not bright sulphur yellow -----u
- u. Pileus yellowish brown; mouths of the tubes almost 1 mm. in diameter; the walls thin -----16. *P. arcularius*
- u. Pileus darker than above, brown or sooty-black; pores smaller, averaging 2 per mm.; walls at first thick -----17. *P. brumalis*
- v. Pileus arising from a cup-shaped sterile body; found only on dead elm branches -----*Polystictus conchifer*
- v. Pileus not as above -----w
- w. Hymenium bright sulphur yellow -----2. *P. sulphureus*
- w. Hymenium not bright sulphur-yellow -----x
- x. Margin of pileus projecting .5 mm. or more beyond the hymenium, found growing on birch -----14. *P. betulina*
- x. Not as above -----y
- y. Hymenium more or less smoke-colored or black when fresh -----z
- y. Hymenium not at all smoke-colored or black when fresh -----bb
- z. Pileus rather thick; hymenium pallid to smoky; dissepiments thick; tramal tissue hyaline or nearly so in cross section -----18. *P. fumosus*
- z. Pileus thinner; hymenium black or smoky; dissepiments thin; tramal tissue decidedly brown in cross section -----aa
- aa. Pileus finely tomentose, margin even; pores minute; pilei slightly or not at all imbricate -----19. *P. adustus*
- aa. Pileus fibrillose on the margin, strigose toward the base; margin crisped and wavy; pores 3-5 per mm. -----20. *P. crispus*

- bb. Pileus distinctly brown or blackish brown in color; context light brown -----21. *P. resinosus*
- bb. Pileus not as above -----cc
- cc. Pileus thin and coriaceous, not more than 1 mm. thick-----22. *P. planellus*
- cc. Pileus not thin and coriaceous -----dd
- dd. Sporophore mostly resupinate -----23. *P. semipileatus*
- dd. Sporophore not mostly resupinate -----ee
- ee. Pileus thin and coriaceous, often zonate, never more than 1.5 cm. thick -----ff
- ee. Pileus either soft and watery or firm and corky (never coriaceous) when fresh, usually more than 1.5 cm. thick -----ii
- ff. Hymenium tinted flesh-color when fresh; sporophore becoming rigid on drying; spores globose -----24. *P. rigidus*
- ff. Hymenium not flesh-colored; not rigid when dry; spores cylindric -----gg
- gg. Hymenium soon breaking up into teeth -----25. *P. tulipiferus*
- gg. Hymenium not breaking up into teeth -----hh
- hh. Dissepiments thick and entire; pileus hirsute, tubes not more than 2 mm. long -----26. *P. hirsutus*
- hh. Dissepiments thin, velvety to pubescent, tubes more than 2 mm. long -----27. *P. pubescens*
- ii. Sporophore growing only on wood of coniferous trees; tubes 3-10 mm. long; pileus hispid to tomentose -----28. *P. borealis*
- ii. Sporophore growing only on wood of deciduous trees -----jj
- jj. Sporophore with a very disagreeable odor when fresh; context hard and bony when dry -----29. *P. Spraguei*
- jj. Sporophore without disagreeable odor when fresh -----kk
- kk. Margin of pileus thick and rounded -----ll
- kk. Margin of pileus thin, not rounded -----mm
- ll. Tubes large, 1 mm. or more in diameter, found growing only on oak -----30. *P. obtusus*
- ll. Tubes much smaller -----31. *P. occidentalis*
- mm. Pileus gray when fresh -----32. *P. tephroleucus*
- mm. Pileus pure white, slightly gray, or yellowish when fresh -----nn
- nn. Spores cylindric-oblong, often allantoid -----oo
- nn. Spores ellipsoid to globose -----qq
- oo. Pileus villous-strigose, hymenium often bluish or grayish blue -----33. *P. caesius*
- oo. Pileus glabrous or slightly pubescent -----pp
- pp. Hyphae of context simple or very slightly branched; pileus usually thick, convex or unguulate, and triangular in section; tubes 4-9 mm. long -----34. *P. albellus*
- pp. Hyphae of context branch greatly; pileus thin and spreading, 0.5-1.5 cm. thick; tube 1.5-3 mm. long -----35. *P. chioneus*
- qq. Sporophore with a sweet acid odor when fresh; surface of pileus conspicuously pubescent, often strigose tomentose at the base -----36. *P. galactinus*

- qq. Sporophore without a sweet fragrant odor when fresh -----rr
 rr. Tubes less than 0.5 cm. long -----37. *P. epileucus*
 rr. Tubes 0.5 cm. or more long -----ss
 ss. Context drying soft crumbly -----38. *P. iowensis*
 ss. Context not drying soft and crumbly -----tt
 tt. Pileus strigose-tomentose or strigose-hispid, especially on the margin; tubes collapsing on drying; mouths equal, small, averaging 3-4 per mm. -----39. *P. spumeus*
 tt. Pileus glabrous or floccose-tomentose; tubes scarcely collapsing when dry, the mouths usually somewhat sinuous, averaging 1-2 per mm. -----40. *P. delectans*
 uu. Context yellowish red, reddish, or orange; spores hyaline -----vv
 uu. Context umber, cinnamon, brown, or ferruginous; spores hyaline or brown -----yy
 vv. Pileus and hymenium deep cinnabar-red -----ww
 vv. Pileus and hymenium not deep cinnabar-red -----xx
 ww. Pileus less than 5 mm. thick, often zonate -----41. *P. sanguineus*
 ww. Pileus more than 5 mm. thick, never zonate -----42. *P. cinnabarinus*
 xx. Hymenium sulphur-yellow or reddish-yellow when fresh -----
 -----2. *P. sulphureus*
 xx. Hymenium not as above, pileus buff or yellowish-orange, growing only on wood of *Quercus* and *Castanea* -----43. *P. croceus*
 yy. Sporophore stipitate -----zz
 yy. Sporophore sessile -----ddd
 zz. Surface of pileus distinctly incrustated -----*Fomes lobatus*
 zz. Surface of pileus not incrustated -----aaa
 aaa. Context not more than 1 cm. thick; pilei growing on the ground -----
 -----bbb
 aaa. Context more than 1 cm. thick; pilei growing on wood or attached to burned wood -----ccc
 bbb. Surface of pileus shining with silky striations -----
 -----*Polystictus cinnamomeus*
 bbb. Surface of pileus not shining, dull -----*Polystictus perennis*
 ccc. Context duplex; spores hyaline under the microscope -----44. *P. circinatus*
 ccc. Context not duplex; growing on stumps or trunks of pine trees -----
 -----45. *P. Schweinitzii*
 ddd. Pilei forming a densely imbricate, globose, or cylindric mass of closely overlapping pilei arising from a central solid core -----46. *P. graveolens*
 ddd. Pilei not as above -----eee
 eee. Pileus distinctly incrustated -----*Fomes lobatus*
 eee. Pileus not incrustated -----fff
 fff. Sporophore growing on stumps of pine trees or wood -----
 -----45. *P. Schweinitzii*
 fff. Sporophore growing on deciduous stumps, shrubs or trees; often on living trunks -----ggg
 ggg. Context very light brown, scarcely colored -----21. *P. resinosus*

- ggg. Context yellowish brown to umber brown or rusty brown ---- hhh
 hhh. Setae none, pileus often soft and watery, usually growing
 on oak wood ----- 47. *P. nidulans*
 hhh. Setae present, sometimes very scarce, either between basidia
 or imbedded in the tramal tissue ----- iii
 iii. Setae-like bodies imbedded in the tramal tissue only; pores greenish
 yellow when fresh; on maple wood ----- 48. *P. glomeratus*
 iii. Setae projecting between the basidia ----- jjj
 jjj. Hyphae 3-4.5 μ ----- kkk
 jjj. Hyphae 5-10 μ ----- ll
 kkk. Pileus very thin; often radiate, zonate ----- 49. *P. licnoides*
 kkk. Pileus of medium thickness; never radiate, not strongly zonate ----
 ----- 50. *P. gilvus*
 ll. Pileus hirsute; growing on various deciduous trees; no central
 core; spores brown ----- 51. *P. hispidus*
 ll. Pileus fibrillose or glabrous; growing on oak wood or trees;
 with a central solid granular core; spores brown -----
 ----- 52. *P. Rheades*

1. *P. umbellatus* Pers. ex Fr.

Fig. 46

Pileus fleshy to tough, stipitate, umbilicate, 7-20 cm. in diameter, stipe branching repeatedly and giving rise to many centrally attached pilei more or less depressed, 1-4 cm. broad, white to smoky brown, fibrillose to glabrous; context white, not more than 1 mm. thick, fragile, when dry; tubes less than 2 mm. long, decurrent, mouths white, angular, averaging 2-4 per mm.; stipe arising from an underground tuber, branches cylindric in form, central or subcentral, white entirely covered by decurrent tubes; spores hyaline, smooth, cylindric, 7-9.5 x 2.5-3.5 μ ; cystidia none; hyphae 2-6 μ .

On stumps and trees.

Syn. *Griofola ramossissima* Scop. ex Murrill.

2. *P. sulphureus* Bull. ex Fr.

Fig. 47

Pileus fleshy and watery, sessile or attenuate to a stemlike base, appearing substipitate, bright orange or yellow soon becoming pale to white with age, nearly glabrous, rather roughened with ridges, 5-20 x 4-12 x 0.5-5 cm.; context white or yellowish, 0.4-4 cm. thick, cheesy; tubes 1-4 mm. long, mouths bright sulphur yellow when fresh and fading with age, angular, averaging 2-4 per mm., spores hyaline, smooth,

ovoid to subglobose, 5-7 x 3.4-5 μ ; cystidia none; hyphae branching, 3-9 μ .

On stumps and trunks of deciduous trees, also on coniferous trees. Common.

Syn. *Laetiporus speciosus* Batt. ex Murrill; *Polyporus cincinnatus* Morgan.

One specimen in the State University of Iowa Herbarium seems to be the white variety, *Polyporus sulphureus* var. *albolabyrinthiporus* Rea.

3. *P. heteroclitus* (Bolt.) Fr.

Pileus expanded horizontally on all sides from a radical tubercle, up to a foot in diameter, caespitose, coriaceous, pilei 6 cm. broad, lobed, orange, villose, azonate; context lighter than outside pilei; tubes golden yellow, short; mouths yellow, becoming brownish, irregular and elongated.

On ground or base of a tree or stump. Probably the same as *P. sulphureus*.

4. *P. Berkeleyi* Fr.

Fig. 63

Sporophore stipitate and composed of from 2-5 broad pilei, or simple with but one large centrally depressed pileus; pilei fleshy-tough, becoming hard and corky, very broad, 6-15 cm., 0.5-1.5 cm. thick, whitish to yellowish, nearly glabrous or finely tomentose, sometimes subzonate, rugose-undulate, margin acute, often inflexed; context white, tough, milky in young specimens; tubes 2-8 mm. long, decurrent, the mouths white or whitish, angular, unequal, large, 0.5-2 mm. broad; very fragile when dry; stem short and thick, more or less tubercular, sometimes, at least, arising from an underground sclerotium or tuber, the portion above ground 4-7 cm. long, 3-5 cm. thick; spores globose, hyaline, echinulate, 5.5-8 μ broad; cystidia none; hyphae simple, 3-4 μ .

Growing around trees and stumps, especially of oak.

Syn. *Grifola berkeleyi* Murrill.

5. *P. frondosus* Dickson ex Fr.

Fig. 48

Pileus fleshy-tough, fibrous, stipitate, very much branched and giving rise to numerous overlapping pilei, forming a more

or less globose mass, as much as 60 cm. across, pilei flabelliform or spatulate, surface grayish or drab, nearly glabrous, 2-7 cm. broad by 2-5 mm. thick; context white, not more than 2 mm. thick, tough; tubes 2-3 mm. long, decurrent, mouths white, angular, unequal, averaging 1-3 per mm.; stipes all united into a very short trunk; spores hyaline, smooth, ovoid or elliptic, 5-9 x 4.5-6 μ ; cystidia none; hyphae simple, 3-8 μ .

On or around stumps of trees.

"*Polyporus anax* Berk. does not seem to differ from *frondosus* except in the larger, irregular pores; both are probably forms of the ancient species *intybaceus*." Morgan.

The species *frondosus* is separated from *umbellatus* by the spatulate pilei in contrast with the orbicular pilei, and the flattened stipe branches in contrast with the cylindric stipe of *umbellatus*.

6. *P. giganteus* Pers. ex Fr.

Fig. 49

Pileus fleshy-tough to subcoriaceous, stipitate, composed of a few broad fleshy pilei, dimidiate, flabelliform or spatulate, brown or grayish, often blackish when dry, tomentose to fibrillose, margin thin and acute, recurved on drying, 6-15 cm. in diameter, 0.5 cm. or less in thickness; context white, 1-3 mm. thick; tubes 1-3 mm. long, mouths white to tannish or pallid, becoming blackish where bruised or on drying, angular, irregular, becoming lacerate, 5-7 per mm.; stipe short and thick; spores hyaline, smooth, globose, 4-8 μ ; cystidia none; hyphae nearly simple, 5-8 μ .

On ground around stumps.

Syn. *Grifola sumstinii* Murrill.

7. *P. pocula* Schw. ex Berk. and Curtis

Fig. 50

Pileus coriaceous when fresh, rigid when dry, stipitate, whitish to brown, pruinose or mealy, azonate, pendant from dead branches, 1-5 mm. broad, 1-3 mm. thick; context white, less than 1 mm. thick; tubes 0.5 mm. or less long, mouths whitish or brownish, at first pruinose, circular, very minute, entire, averaging 5-7 per mm.; stipe attached at vertex, expanded into the pileus, pruinose, short, not more than 5 mm.

long; spores hyaline, smooth, globose, 4-5 μ , a few cylindric shaped spores were also found, 4.5-5 x 0.7-1 μ ; cystidia none; hyphae simple to branched, 4-5 μ .

On dead branches of oak, chestnut, etc.

Syn. *Polyporus cupulaeformis* Berk. ex Fr.; *Sphaeria pocula* Schw.; *Porodisculus pendulus* (Schw.) Murrill; *Porodiscus pendulus* Murrill.

8. *P. distortus* Schw. ex Fr.

Pilei fleshy-tough to coriaceous, confluent, usually wholly distorted and almost the entire surface covered with pores, stipitate or substipitate when well developed, orbicular, white to tan, villous-tomentose, 2-10 cm. broad, 0.5-1.5 cm. thick; context white, duplex when mature, 0.2-1 cm. thick; tubes 1-6 mm. long, mouths whitish or pallid, brown when dry, minute, angular to daedaloid, averaging 1-3 per mm.; stipe central, lateral or wanting, usually rudimentary and tubercular; spores hyaline, smooth, ellipsoid to subglobose, 5-7 x 3.5-5 μ ; cystidia present or absent, hyaline, blunt, 20-40 x 6-10 μ ; hyphae simple, 5-8 μ .

On dead wood of deciduous trees.

Syn. *Polyporus abortivus* Peck.

9. *P. radicans* Schw.

Fig. 53

Pileus fleshy-tough, stipitate, orbicular, convex to depressed, yellowish brown or reddish brown, subsquamulose or fibrillose scaly, tomentose, 3.5-20 cm. broad, 3-9 mm. or thicker; context white or cream, 3-6 mm. thick or thicker near center, soft, spongy; tubes 1-5 mm. long, decurrent, mouths white to isabelline, circular, 2-3 per mm.; stipe central, velvety or squamulose with a long black root, 6-13 cm. long, 0.5-2 cm. thick; spores hyaline or light yellow, smooth, ovoid-elliptic or subfusiform, 12-15 x 6-8 μ ; cystidia none; hyphae 4-8 μ .

On ground often around stumps.

Syn. *Polyporus morgani* Peck; *Polyporus kansensis* Ellis and Barth.

10. *P. varius* Fr.

Fig. 51

Pileus fleshy-tough, stipitate, thin, becoming woody, brown, slightly streaked with fine lighter radiating lines, glabrous,

margin thin; context white, less than 1 mm. thick; tubes 1 mm. or less long, decurrent, mouths whitish, then cinnamon-brown, round, unequal, 5-6 per mm.; stipe excentric, lateral or wanting, short, smooth, becoming black at the base; spores hyaline, smooth, oblong, $5-7.5 \times 2-3 \mu$; cystidia none; hyphae simple, slightly branched.

On trunks and branches of deciduous trees.

11. *P. squamosus* Hudson ex Fr.

Fig. 52

Pileus somewhat fleshy when fresh, corky tough to firm when dry, short stipitate or almost sessile, whitish to dingy yellowish or brownish, covered with large appressed brownish scales, 6-25 cm. broad, 0.5-4 cm. thick; context white, thick, 0.5-3.5 cm.; tubes 2-8 mm. long, decurrent, mouths white or yellowish, large, angular, 1-2.5 mm. broad; stipe excentric or lateral, reticulate above, thick, black at the base, 1-5 cm. long; spores hyaline, smooth, oblong-cylindric, $10-14 \times 5-5.5 \mu$; cystidia none; hyphae branched, $2-8 \mu$.

On living wood of deciduous trees. Found abundantly on maple trees in Iowa.

Syn. *Polyporus caudicinus* Scop. ex Murrill.

12. *P. elegans* Bull. ex Fr.

Fig. 54

Pileus coriaceous when fresh, soon hardening, stipitate, convex or nearly plane, orbicular or reniform, surface often distinctly radiate-striate, pruinose to glabrous, pale ochraceous or dull orange, margin thin, at first inflexed, becoming wavy or much lobed with age, $2-6 \times 3-10 \times 0.2-1$ cm.; context white to pallid, 1-6 mm. thick; tubes 1-3 mm. long, decurrent, mouths whitish to avellaneous, angular to subcircular, averaging 4-5 per mm.; stipe eccentric or entirely lateral or central, woody, smooth, pallid above, abruptly black at the base, 1-8 cm. long, 0.2-0.6 cm. thick; spores hyaline, smooth, cylindric, $6-8 \times 2.5-3.5 \mu$; cystidia none; hyphae branching, $2-5 \mu$.

On fallen branches and trunks of deciduous trees.

This species is regarded by some as only a form of *P. picipes*.

Syn. *Polyporus fissus* Berk.

13. *P. picipes* Fr.

Fig. 55

Pileus thin, coriaceous and pliant when fresh, becoming rigid stipitate, convex to depressed or infundibuliform, chestnut brown or reddish brown, glabrous, center often darker than margin, margin thin, 4-20 cm. broad; context white to pallid, 1-7 mm. thick; tubes up to 2 mm. long, decurrent, mouths white to brownish, small, averaging 5-7 per mm.; stipe central or eccentric, black at the base, glabrous, 1-6 cm. long, 0.4-1.5 cm. thick; spores hyaline, smooth, cylindric, elliptic, $6-8 \times 2-3 \mu$.

On stumps and logs of deciduous trees.

This species differs from *P. elegans* in the much darker color, more lateral stipe, and usually smaller size. Some regard *P. elegans* as only a form, but to me it seems quite distinct.

14. *P. betulinus* Bull. ex Fr.

Pileus fleshy or corky, sessile or attached by a short umbo behind, compressed-ungulate, convex above, plain below, surface covered with a thin, brown or smoky separating pellicle, glabrous, margin incurved, obtuse and rounded, projecting beyond hymenium nearly 1 cm., $3-15 \times 3-20 \times 2-5$ cm.; context white, 1-3.5 cm. thick, fleshy tough, homogeneous; tubes 3-8 mm. long, separating in a layer from the context, mouths very irregular, white, dissepiments thick, averaging 2-4 per mm.; spores hyaline, smooth, cylindric, curved, $6 \times 2.5 \mu$; cystidia none; hyphae mostly simple, nodulose, 3-5 μ .

Growing only on birch trees.

Syn. *Piptoporus suberosus* Linn. ex Murrill.

15. *P. osseus* Kalch.

Pileus fleshy tough when fresh, very rigid and firm when dry, imbricate somewhat attenuate to a stemlike base, white or gray, nearly glabrous, $1-4 \times 2-8 \times 0.3-1$ cm.; context white, 3-7 mm. thick, firm when fresh, hard when dry; tubes 1-3 mm. long, mouths whitish, averaging 5 per mm.; spores not obtained; cystidia none; hyphae 6-8 μ .

On old oak stumps.

16. *P. arcularius* Batsch ex Fr.

Fig. 56

Pileus tough, coriaceous, stipitate, orbicular to convex, umbilicate, golden brown to dark brown, squamulose or glabrous, concentrically rugose when dry, margin often ciliate, involute on drying, 1-5 cm. broad, 0.1-0.2 cm. thick; context white, 1-2 mm. thick; tubes up to 2 mm. long, decurrent, mouths white or yellowish, brownish when dry, large, angular, 0.5-2 per mm., edges thin; stipe central, yellowish brown or dark brown, fuscous, squamulose, sometimes hispid at base, 1-6 cm. long, 2-4 mm. thick; spores hyaline, smooth, cylindric-elliptic, two or three guttulate, $6-8 \times 2-3 \mu$; cystidia none; hyphae branched, $2-5 \mu$.

On stumps and logs.

17. *P. brumalis* Pers. ex Fr.

Pileus fleshy-tough to rigid, stipitate, orbicular, subumbilicate or infundibuliform, dark brown or blackish, sometimes yellowish-brown, minutely hispid to glabrous, stiff hairs easily rubbed off when dry, margin involute when young and when dry, 1.5-6 cm. broad, 0.2-0.4 cm. thick; context white, 3 mm. or less thick; tubes 1-3 mm. long, slightly decurrent, mouths whitish to pallid, circular, thick walled, then angular and thinner, 2-3 per mm.; stipe central or nearly so, grayish or brownish, slender, minutely hispid, solid, equal, 2-3 cm. long, 0.2-0.3 cm. thick; spores hyaline, smooth, oblong, $7-9 \times 2-3 \mu$; cystidia none, but scattered columnar tufts of projecting hyphae; hyphae simple or branched, $2-4 \mu$.

On dead wood.

Syn. *Polyporus polyporus* (Retz) Murrill.

18. *P. fumosus* Pers. ex Fr.

Fig. 57

Pileus fleshy, coriaceous, corky or rigid, sessile or effused-reflexed, white to ochraceous or smoky white, pallid or light brown when dry, finely tomentose to glabrous, azonate, $1-6 \times 3-8 \times 0.1-0.6$ cm.; context white to fibrous, subzonate, 2.5-10 mm. thick, separated from hymenophore by a very narrow dark line, anise-scented, or with a disagreeable odor; tubes 1.5-4 mm. long, mouths small, white to yellowish or grayish

black, becoming darker when bruised, round to angular, averaging 3-5 per mm.; tramal tissue hyaline or nearly so under microscope; spores hyaline, smooth, $4.5-6 \times 2-3 \mu$; cystidia none; hyphae simple to slightly branched with clamp connections $3-6 \mu$.

On dead wood of deciduous trees.

Syn. *Bjerkandera fumosa* (Pers.) Karst.; *Polyporus fragrans* Peck.

19. *P. adustus* Willdenow ex Fr.

Fig. 58

Pileus fleshy-tough, corky, sessile, effused or effused-reflexed, slightly or not at all imbricate, white to cream, gray, or cinereous-pallid, finely tomentose, azonate, margin thin, even, often black when dry, sterile below, sterile margin being more or less light colored, $1-6 \times 3-7 \times 0.1-0.8$ cm.; context white to pallid, 1-5 mm. thick, corky when dry, usually separated from hymenial layer by a dark line; tubes less than 2 mm. long, mouths grayish black to black, very minute, round, averaging 6 per mm.; tramal tissue brown under microscope; spores hyaline, smooth, oblong, rarely slightly curved, $3.5-5 \times 1.5-2.5 \mu$; cystidia none; hyphae hyaline, rarely branched, $3-5 \mu$.

Common on dead deciduous wood.

This species is distinguished from *P. fumosus* by the darker pores and the brown color of the tramal tissue; from *P. crispus* by the even margin and less imbricate pilei.

20. *P. crispus* Pers. ex Fr.

Pileus coriaceous, sessile or effused-reflexed, dimidiate, closely imbricate, gray or avellaneous, adpressedly fibrillose toward margin and usually strigose toward base, margin thin, crisped or wavy, sometimes becoming black, sterile below, $1-4 \times 1-7 \times 0.1-0.4$ cm.; context white, 1-3 mm. thick, corky, occasionally separating from the hymenium by a narrow dark line; tubes less than 1 mm. long, mouths gray, unequal, averaging 3-6 per mm.; tramal tissue decidedly brown in color under microscope; spores hyaline, smooth, oblong, $3.5-4.5 \times 1.5-2.5 \mu$; cystidia none; hyphae nearly simple, $4-6 \mu$.

On dead wood of deciduous trees.

21. *P. resinosus* Schrader ex Fr.

Fig. 59

Pileus fleshy and watery when young, flesh becoming corky when mature, hard when dry, sessile or reflexed, cinnamon brown to darker brown, velvety-tomentose to glabrous, slightly resinous, zonate with darker colored bands, 5-15 x 7-25 x 1-2.5 cm.; context tan or very light brown, 0.5-2 cm. thick; tubes 1-7 mm. long, mouths white to pallid, becoming darker on being bruised or drying, 4-6 per mm.; spores hyaline, smooth, cylindric, or allantoid, 4-6 x 1-2 μ ; cystidia none; hyphae simple 3-6 μ .

Syn. *Polyporus fuscus* Pers.; *Ischnoderma fuliginosum* Scop. ex Murrill.

22. *P. planellus* Murrill

Pileus very thin, coriaceous, narrowly attached, sessile or effused-reflexed, finely tomentose to glabrous, multizonate, light brown to umber, the zones darker, 1-3.5 x 1-3 x 0.05-0.1 cm.; context papery-thin, whitish; tubes less than 1 mm. long, the mouths white or yellowish, angular, averaging 5-6 per mm.

On dead limbs of deciduous trees.

The above description was adapted from Overholts.

Syn. *Polyporus planus* Peck.

This species should more properly be placed in the genus *Polystictus*. It is, however, doubtful whether it occurs in Iowa. Fennell has listed it among the Iowa species. No specimen has been seen.

23. *P. semipileatus* Peck

Pileus spongy and watery when fresh, tough and hard when dry, very narrowly reflexed or effused-reflexed, largely resupinate, white, yellowish or brownish, azonate, glabrous to slightly tomentose, margin thin, sometimes inflexed, 0-1.5 x 0.7-3.5 x 0.1-0.5 cm.; context white, 1-4 mm. thick, fleshy-tough to fragile; tubes short, less than 2 mm. long, mouths white to yellowish, often bluish-discolored in spots, circular, angular, averaging 4-7 per mm., dissepiments thin, even, entire; spores hyaline, smooth, slightly allantoid, 3-4 x 1 μ ; cystidia none or of tufts of hyaline projecting hairs; hyphae hyaline, roughened along edge, simple, 2-4 μ .

On dead wood of deciduous trees.

Syn. *Polyporus semisupinus* Berk. ex Curtis.

24. *P. rigidus* Leveille

Fig. 64

Pileus fleshy and pliant when fresh, rigid and firm when dry, sessile, dimidiate or laterally confluent, effused-reflexed or entirely resupinate, whitish to flesh-colored or isabelline, very finely tomentose to glabrous, azonate to zonate when mature, somewhat rugose, margin obtuse, then thin, 0-0.5 x 1-3 x 0.2-2.5 cm.; context white, 1-5 mm. thick, hard and rigid when dry; tubes 1-4 mm. long, mouths flesh-tinted to cream, angular, averaging 4-5 per mm., walls thick and entire; spores hyaline, smooth, globose, 2.5-5 μ broad; cystidia none; hyphae simple, 5-7 μ .

On dead logs, especially of poplar.

Syn. *P. zonalis* Berk.

25. *P. tulipiferus* Schw. ex Overholts

Fig. 61

Pileus coriaceous, thin, sessile, effused-reflexed or resupinate, white or whitish, villous, zonate, 0-1 x 1-5 x 0.1-0.6 cm.; context white 0.5-2 mm. thick; tubes 1-5 mm. long, mouths white or yellowish, soon breaking up into teeth, averaging 2-3 per mm; spores hyaline, smooth, cylindric, allantoid, 4.5-5 x 1-2 μ , spores print slightly greenish, spores 2 guttulate; cystidia scattered, encrusted, having a greenish cast, 35-45 x 10-20 μ , projecting 15-30 μ ; hyphae slightly branched, 4-6 μ .

On dead wood of deciduous trees, on elm, etc.

Syn. *Irpex lacteus* Fr.; *Irpiciporus lacteus* (Fr.) Murrill.

The description of *Polystictus arcticus* Fr. as given by Macbride seems to suggest that it is only a synonym of *Polyporus tulipiferus*.

26. *P. hirsutus* Wulfen ex Fr.

Fig. 62

Pileus coriaceous, flexible or rigid, more or less imbricate, sessile or reflexed, grayish yellowish or brownish, densely hirsute or tomentose, concentrically furrowed, zonate, zones not variously colored, margin thin, sometimes with a narrow sterile margin, 1.5-5 x 1.5-7 x 0.2-1 cm.; context white, 1-6

mm. thick, fibrous, spongy above; tubes 1-4 mm. long, mouths white to yellowish or smoky, circular to angular, entire, averaging 3-4 per mm.; spores hyaline, smooth, $5-8 \times 1.5-2.5 \mu$; cystidia none; hyphae simple, $2-7 \mu$.

On dead deciduous wood.

Syn. *Coriolus nigromarginatus* (Schw.) Murrill; *Polystictus hirtellus* Fr.

27. *P. pubescens* Schumacher ex Fr.

Pileus coriaceous or fleshy-tough when fresh, sessile, dimidiate or flabelliform, conchate, white or yellowish (rarely umber) villous tomentose to finely tomentose, finely radiate-lineate in front at times, $1.5-5 \times 2.5-5 \times 0.4-1$ cm.; context white, 1-5 mm. thick, fibrous; tubes 1-4 mm. long, mouths yellowish white to umber, angular, averaging 3-4 per mm., dissepiments thin, often dentate; spores hyaline, smooth, cylindric or allantoid, $5-6 \times 1.5-2.5 \mu$; cystidia none; hyphae nearly simple, $5-8 \mu$.

On stumps and old trunks of deciduous wood.

One specimen in the State University of Iowa Herbarium collected by Holway is referred by Macbride to the variety *Grayii* Ellis and Everhart N. A. F. 1933.

Syn. *Polyporus Sullivantii* Mont.

28. *P. borealis* Fr.

Pileus soft but tough and watery when fresh, sessile, white or yellowish, hispid to tomentose, context white, firm and fibrous next the hymenium, soft and floccose above, $3-8 \times 4-12 \times 0.5-2.5$ cm.; tubes 3-10 mm. long, mouths white or yellowish, angular to daedaloid, uneven, averaging 2-3 per mm.; spores hyaline, smooth, ellipsoid to oval, $4-5 \times 3-4 \mu$; cystidia abundant, hyaline or brown, ventricose, $24-30 \times 8-10 \mu$, projecting but slightly beyond the basidia; hyphae simple, $5-7 \mu$.

On trunks of coniferous trees.

The above description is adapted from Overholts.

There seems to be no specimen in the State University of Iowa Herbarium. Reported by Fennell.

Syn. *Spongipellis borealis* Murrill.

29. *P. Spraguei* Berkeley and Curtis

Fig. 60

Pileus watery and more or less soft when fresh, fleshy tough, sessile or attenuate behind, convex, white or gray, finely tomentose to glabrous, slightly tuberculose, azonate, margin often blackening with age, 4-12 x 4-15 x 0.6-3 cm.; context white, woody when dry, 0.3-1.5 cm. thick, disagreeable odor when fresh; tubes 0.3-1 cm. long, mouths white becoming brownish with age and on drying, angular, 3-4 per mm., white to yellowish within; spores hyaline, smooth, ellipsoidal, or subglobose, 4-5 μ ; cystidia none; hyphae hyaline, somewhat branched, 4-7 μ .

On dead wood of deciduous trees.

Syn. *Polyporus sordidus* Cooke; *Tyromyces spraguei* (Berk. and Curtis) Murrill.

30. *P. obtusus* Berk.

Fig. 67

Pileus spongy to firm, sessile, somewhat imbricate, dimidiate, often unguulate, surface sordid white to isabelline or fulvus, spongy-tomentose or hispid-tomentose, azonate, margin thick, 3-9 x 4-15 x 3-6 cm.; context white or pallid with age, 1-4 cm. thick, spongy fibrous; tubes 1-3 cm. long, white to isabelline within, mouths white to isabelline, later bay and resinous in appearance, large, circular to angular to irregular, often sinuous, compound, fimbriate, dentate to slightly lacerate, 1 mm. or more in diameter; spores hyaline, smooth, subglobose, 6-8 x 4-6 μ ; cystidia none; hyphae somewhat branched, 5-6 μ .

On trunks of deciduous trees, especially oak.

Syn. *Spongipellis unicolor* (Schw.) Murrill; *Polyporus tomentosus* Johnson; *Daedalea obtusa* Berk.

31. *P. occidentalis* Murrill ex Sacc.

Pileus spongy, thick, sessile, white to yellowish, hispid-tomentose; 5-8 x 7-10 x 2-3 cm.; margin very thick and rounded; context white to slightly yellowish, 1-2 cm. thick; tubes 1 cm. long, the mouths white to yellowish, minute, angular, averaging 5 per mm., the dissepiments becoming lacerate and collapsing; spores ellipsoid, smooth, hyaline, 6-7 x 4-5 μ ; cystidia none; hyphae 6 μ .

On old logs in woods.

The above description is adapted from Overholts, who has reported this species only for Iowa.

There seems to be no specimen in the State University of Iowa Herbarium. The species is very similar to *P. obtusus* except for the much smaller pores.

32. *P. tephroleucus* Fr.

Pileus soft and watery when fresh, rigid when dry, applanate, avellaneous or decidedly gray, glabrous or nearly so, 1-7 x 2-8 x 0.5-1.5 cm.; context white, 3-10 mm. thick; tubes 2-7 mm. long, the mouths white or whitish, angular, averaging 4-5 per mm.; spores hyaline, smooth, allantoid, 4-5 x 0.6-1.5 μ ; cystidia none.

On dead wood of deciduous trees. Not uncommon on rotten logs in marshy places.

The grayish pileus separates this species from *P. albellus*.

33. *P. caesius* Schrad. ex Fr.

Pileus soft and watery when fresh, rigid when dry, sessile or effused-reflexed, dimidiate, whitish to grayish, often bluish tinted, villose-pubescent or tomentose, azonate; margin thin and acute; context white, 3-10 mm. thick; tubes 2-7 mm. long, mouths white or grayish blue, unequal, angular, 1-5 per mm.; dissepiments thin and lacerate; spores hyaline, smooth, cylindric or allantoid, 3-5 x 1-1.5 μ ; cystidia none; hyphae simple, 5-7 μ .

On dead wood of deciduous and coniferous trees.

34. *P. albellus* Peck

Fig. 65

Pileus soft and watery when fresh, sessile, dimidiate, somewhat imbricate, convex, more or less triangular in sections, surface grayish cinereous, or yellowish-white, azonate, sodden, pubescent, glabrous or slightly pubescent, covered with a thin pellicle which is more apparent in dried specimens, 1-5 x 1-10 x 1-6 cm.; context white, soft and watery, with a mild acid odor when fresh, when dry homogeneous, mealy and fragile, cutting with a smooth surface, 0.5-3 cm. thick; tubes 4-10 mm. long, mouths white or yellowish, angular or rounded,

grayish, averaging 3-5 per mm.; spores hyaline, smooth, cylindrical or allantoid, $3.5 \times 1.5 \mu$; cystidia none; hyphae simple, clamp connections present, $4-7 \mu$ broad.

On dead wood of deciduous trees.

Syn. *Polyporus lacteus* Fr.; *Tyromyces chioneus* Murrill.

35. *P. chioneus* Fr.

Pileus soft and watery when fresh, thin and appanate, sessile or effused-reflexed, white, grayish or yellowish on drying, covered with a thin gray or yellowish pellicle that is more evident in dried specimens, $2.7 \times 1.5 \times 0.5-1.5$ cm.; context white, usually fragrant when fresh, friable when dry, 2-7 mm. thick; tubes 1.5-3 mm. long, the mouths white or yellowish, angular, averaging 3-4 per mm., the walls nearly entire; spores cylindrical or allantoid, smooth, hyaline, $3.4 \times 0.7-1.5 \mu$; cystidia none; hyphae much branched, $4-8 \mu$.

On dead wood of deciduous and coniferous trees

The above description is adapted from Overholts. There seems to be no specimen in the State University of Iowa Herbarium.

Reported from Iowa by Macbride.

36. *P. galactinus* Berk.

Pileus soft and watery when fresh, sessile, white or yellowish, strigose-tomentose at base, short-tomentose on the margin, $3.8 \times 5.10 \times 1.3$ cm.; context white, hard and sometimes resinous when dry, 0.3-2 cm. thick, strongly zonate, with a peculiar fragrant odor when fresh; tubes 5-10 mm. long, the mouths white or yellowish, angular, averaging 4-6 per mm.; spores ellipsoid, smooth, hyaline, 1-guttulate, $3.4 \times 2.3 \mu$; cystidia none; hyphae simple, $4-6 \mu$.

On old logs in woods, especially in overflow river bottoms.

Syn. *Polyporus immitus* Peck.

37. *P. epileucus* Fr.

Pileus soft and watery when fresh, sessile or effused-reflexed, white or yellowish, drying ochraceous, nearly glabrous but rugose, $1.2 \times 1.5-5 \times 1.3-1.6$ cm.; context white, firm, tough, 1-4 mm. thick; tubes 1-3 mm. long, the mouths white or yellowish, averaging 2-4 per mm.; spores (teste Lloyd) hyaline, smooth, reniform, $5 \times 2.5 \mu$; cystidia none.

On dead wood of deciduous trees.

The above description is adapted from Overholts.

There seems to be no specimen in the State University of Iowa Herbarium. Reported by Macbride.

38. *P. iowensis* Lloyd

Fig. 66

Pileus fleshy when fresh, sessile, white, surface anoderm, smooth, dull, margin thin; context white, 0.2-1 cm. thick, when drying crumbly; tubes 0-1 cm. long, mouths small, irregular, surface drying slightly yellowish; spores hyaline, smooth, subglobose, 4-5 x 2.5-3 μ ; cystidia none; hyphae simple to branched, clamp connections present, 4-6 μ .

This is close to *Polyporus galactinus* which, however, has a pubescent surface when fresh, dries hard and discolors.

39. *P. spumeus* Sowerby ex Hornemann

Pileus soft and watery when fresh, sessile, white or somewhat yellowish, villous-strigose or matted strigose-tomentose, 5-20 x 6-20 x 2-6 cm.; context white, 1-3 cm. thick; tubes 0.5-1.5 cm. long, the mouths white or yellowish, angular, averaging 2-4 per mm., the dissepiments thin and acute, collapsing; spores ellipsoid to subglobose, smooth, hyaline, 5-6 x 4-5 μ ; cystidia none; hyphae simple, 4-6 μ .

Growing from wounds in living trees, rarely on logs.

The above description is adapted from Overholts.

Reported by Overholts. This species was not seen or studied. Murrill (26) states that this species is considered by some to be the same as *P. galactinus*.

40. *P. delectans* (Peck) Murrill

Fig. 68

Pileus soft and watery when fresh, fleshy-fibrous to corky when dry, sessile or effused-reflexed, dimidiate or convex, white or slightly yellowish, glabrous or finely tomentose, azonate, margin thin, acute, 3-15 x 5-20 x 1.5-5 cm.; context white, when fresh, 0.5-2 mm. thick, often duplex when dry, spongy above, firm and woody below; tubes 0.5-1.5 cm. long, mouths white to yellowish, large, angular or circular or sinuous, edges thin, entire or slightly dentate; spores hyaline, smooth, subglobose

to ovoid, often 1-guttulate, 5-8 x 4-6 μ , larger than given by Overholts; cystidia none; hyphae simple to slightly branched, 4-5 μ .

Syn. *Spongipellis delectans* (Peck) Murrill.

41. *P. sanguineus* Linn. ex Fr.

Pileus coriaceous, sessile or attenuate at the base and appearing substipitate, bright red, finely tomentose to glabrous, the margin very thin, 2-5 x 2-8 x 0.2-0.5 cm.; context red or yellowish red, floccose, up to 2.5 mm. thick; tubes 0.5-1.5 mm. long, the mouths red, averaging 2-4 per mm.; cystidia none; hyphae nearly simple, 4-6 μ .

On dead wood of deciduous trees.

The above description is adapted from Overholts.

Reported by Fennell. It is a much thinner form than *P. cinnabarinus*.

42. *P. cinnabarinus* Jacquin ex Fr.

Fig. 69

Pileus tough, coriaceous to rigid, sessile, orange to cinnabar red, often paler with age, velvety tomentose to glabrous, 2-6 x 2-10 x 0.5-2 cm.; context red or yellowish red, 0.4-1.5 cm. thick, strongly zonate, floccose-fibrous or soft corky; tubes 1-4 mm. long, mouths cinnabar-red, circular to angular, averaging 2-4 per mm.; spores hyaline, smooth, oblong, 4.5-5.5 x 2-3 μ ; cystidia none; hyphae hyaline to brown, simple, 6-8 μ .

On dead wood of various kinds.

43. *P. croceus* Pers. ex Fr.

Pileus watery, more or less soft when fresh, sessile, dimidiate, convex, surface buff or orange color, fading on drying, rugose, sodden, minutely tomentose to glabrous, margin obtuse becoming thinner at maturity, 5-12 x 6-15 x 1-5 cm.; context pale buff, carneous when dry, conspicuously marked with sordid zones, strong odor, not characteristic, 0.7-2 cm. thick; tubes 0.5-2 mm. long, mouths orange-colored, brownish on drying, angular, averaging 3-5 per mm.; spores hyaline, smooth, ellipsoidal, 3-4 x 2-3 μ ; cystidia none; hyphae simple, 3-5 μ .

On dead oak and chestnut wood.

Syn. *Polyporus pilotae*.

Fennell lists this species as reported by Murrill.

44. *P. circinatus* Fr.

Fig. 73

Pileus subcoriaceous when fresh, stipitate or substipitate, orbicular or flabelliform, plane or depressed in the center, surface velvety, yellowish-brown to ochraceous when mature, white when young, azonate, sterile below, acute, entire to lobed, 3-12 x 0.3-2 cm.; context ochraceous brown, soft and spongy above, firm and woody next to the hymenophore, 1-15 mm. thick; tubes 1.5-4 mm. long, mouths grayish-brown, decurrent, angular, averaging 2-4 per mm.; stipe lateral, central, or rudimentary, tomentose or velvety brown, up to 5 cm. long; spores hyaline under the microscope, colored in mass, smooth, 4-6 x 2-3 μ ; setae abundant, dark brown, pointed, 40-60 x 5-10 μ ; hyphae yellowish to hyaline, 3-10 μ .

On ground or growing on charred wood.

Syn. *Polyporus tomentosus* Fr.; *Coltricia tomentosus* Fr.; *Polyporus dualis* Peck.

45. *P. Schweinitzii* Fr.

Pileus spongy or soft corky when fresh, sessile, dimidiate or irregular, stipitate, surface ochraceous to orange-colored or rusty brown, strigose-tomentose, scrupose in zones or nearly glabrous, margin rather thick, 5-20 cm. broad, 0.5-1.5 cm. thick; context soft spongy when fresh, yellowish to reddish brown, 0.2-1 cm. thick; tubes 1-6 mm. long, mouths yellowish, darker where bruised and on drying, soon irregular, averaging 1-3 per mm.; stipe present or absent, central or lateral, tubercular or very short, concolorous with the pileus, tomentose, soft as the pileus, 0-6 cm. long, 1-2 cm. thick; spores ellipsoid or ovoid, smooth, hyaline, 6-8 x 4-5 μ ; cystidia present, brown, more or less clavate, projecting 30-60 μ , 8-10 μ broad, sometimes knobbed at the apex; hyphae 6-9 μ .

On or about trunks or stumps of pine.

This species is listed by Fennell, but specimens have not been seen from Iowa.

46. *P. graveolens* Schw.

Sporophore made up of numerous overlapping pilei, arising from a solid central core, 5-20 cm. across; pilei corky, rigid, conchate, surface radiate sulcate, slightly zonate, grayish-

brown, cinnamon-brown or grayish-black, pulverulent or glabrous, margin curved concealing pores, 1-3 cm. long, 3-8 mm. thick; context brown, floccose-fibrous, 1-4 mm. thick; tubes 2-4 mm. long, mouths gray-brown to umber, circular, averaging 3-4 per mm.; spores hyaline, smooth, cylindric, 9-10 \times 2.5-3.5 μ ; cystidia none, hyphae sometimes encrusted and projecting from hymenium, rarely branched, 4-8 μ .

On logs and trunks of deciduous trees.

Syn. *Polyporus conglobatus* Berk.; *Fomes conglobatus* Berk.

47. *P. nidulans* Fr.

Fig. 70

Pileus soft and spongy when fresh, sessile, or effused-reflexed, dimidiate, usually broadly attached, sometimes slightly imbricate, surface umber to cinnamon or tawny brown, finely tomentose to fibrillose or glabrous, margin purplish or reddish when bruised, 1.5-6 \times 2-8 \times 0.5-2 cm.; context concolorous with pileus, spongy, friable when dry, 2-8 mm. thick, changes pink with addition of KOH; tubes 2-7 mm. long, mouths yellowish or reddish brown, angular, averaging 3-4 per mm.; spores hyaline, smooth, globose or subglobose, 2-3.5 μ .

On dead wood of deciduous trees, especially on oak.

Syn. *Hapalopilus rutilans* (Pers.) Murrill; *Polyporus rutilans* Pers. ex Fr.; *Polyporus pallido-cerwinus* Schw.

48. *P. glomeratus* Peck

Pileus corky, sessile or effused-reflexed, dark tawny, uneven, minutely velvety-tomentose, 2.5-4 \times 4-8 \times 0.4-1.5 cm.; context 2-7 mm. thick, tawny; tubes 2-7 mm. long, mouths greenish yellow when fresh, brown when dry, angular, averaging 5-6 per mm.; spores yellowish, smooth, subglobose, 5-6 μ ; setae not projecting into tubes, but large, thick, 8-9 μ , deeply colored; long, cylindric seta-like bodies are present in the trama; hyphae 3-4 μ .

On maple logs.

P. glomeratus is reported as occurring in Iowa by Fennell.

49. *P. licnoides* Mont.

Fig. 74

Pileus corky pliable and thin, sessile, or effused-reflexed, grayish brown to cinnamon brown, glabrous, radiate-lineate,

somewhat rugose, zonate, margin thin and acute, 2-6 x 2.5-8 x 0.2-0.7 cm.; context yellowish brown, 1-6 mm. thick; tubes 1-3 mm. long, mouths dark brown, small, averaging 6-8 per mm.; spores hyaline, smooth, 3-4 x 2-2.5 μ ; setae brown, abundant, awl-shaped 13-30 x 4-7 μ ; hyphae simple 3-4 μ .

On dead wood of deciduous trees.

50. *P. gilvus* Schw. ex Fr.

Fig. 75

Pileus coriaceous, corky to woody, firm, sessile, or effused-reflexed, dimidiate, surface yellowish brown or reddish brown, azonate, roughened with warty granules, somewhat zonate, usually glabrous when mature, margin acute, 1-7 x 2-12 x 0.2-2 cm.; context yellowish brown, 0.1-1.3 cm. thick; tubes 1-5 mm. long, mouths dark brown or reddish brown, averaging 6-8 per mm.; spores hyaline, smooth, oblong-ellipsoid, 5 x 3-4 μ ; setae abundant, brown, pointed, awl-shaped, 10-30 x 5-10 μ ; hyphae simple, 3.5-4.5 μ broad.

On dead wood of all kinds.

Syn. *Polyporus isidioides* Berk.; *Polyporus scruposus* Fr.

Polyporus scruposus is regarded as a synonym by Morgan. He is unable to separate them even as varieties. Differences may be based on form and age of specimens.

51. *P. hispidus* Bull. ex Fr.

Pileus soft and watery when fresh, thick, fleshy, sessile, yellowish brown to rusty red, surface covered with a soft dense hirsute or hispid tomentum, azonate, margin obtuse, 6-20 x 9-25 x 2-6 cm.; context spongy-corky, fragile when dry, usually light yellowish brown above and dark reddish brown next the hymenium, 1-1.5 cm. thick; tubes 0.5-1.5 cm. long, mouths yellowish brown becoming darker where bruised and on drying, averaging 2-4 per mm., dissepiments thin; spores smooth, broadly ovoid to ellipsoid, thick walled, yellowish brown, 7-9.5 x 6.5-7 μ ; setae none; long brown seta-like bodies were found in the trama, 80-20 μ ; hyphae 6-10 μ .

On living trunks of deciduous trees.

Syn. *Polyporus endocrocinus* Berk.

The above description was adapted from Overholts.

Polyporus hispidus is closely related to *P. Rheades*. It is dis-

tinguished from that species by the absence of a central globose granular core.

52. *P. Rheades* Pers. ex Fr.

Fig. 76

Pileus somewhat fleshy or spongy when young, firm when dry, thick, sessile, unguulate, sometimes subimbricate, often subglobose or tubercular, surface tomentose, thin innate pubescent, or scabrous, finally almost glabrous, grayish brown to reddish brown, margin thick, sterile, slightly zonate, 3-15 x 4-22 x 2.5-10 cm.; context brown with two definite regions, a central solid globose, granular core, 3-10 cm. thick, often permeated with white mycelial strands, with a brown outer fibrous zone, changes to black with KOH; tubes 0.3-3 cm. long, mouths cinnamon-brown, averaging 2-3 per mm.; spores brown, smooth, ellipsoidal to subglobose, 6-7 x 4-5 μ ; setae present or absent, when present dark brown, sharp pointed, projecting 10-20 μ ; hyphae nearly simple, 5-8 μ .

On living (rarely dead) oak, poplar, and willow.

Syn. *Polyporus dryophilus* (Berk.) Murrill; *Inonatus dryophilus* (Berk.) Murrill.

Tribe IV. Boleteae

Sporophore fleshy, usually perishable, putrescent, the tubes usually easily separable from the pileus in a layer, most forms with a central stipe, annual, usually terrestrial.

KEY TO GENERA

- a. Sporophore very scaly with cone shaped projections, spores dark brown and warty ----- *Strobilomyces*
- a. Sporophore not as above ----- b
- b. Stratum of tubes easily separable from pileus; stipe central ----- *Boletus*
- b. Stratum of tubes not easily separable from the pileus and from each other; tubes of hymenium more or less radiating, adnate or subdecurrent ----- *Boletinus*

Genus STROBILOMYCES Berk.

Sporophore fleshy to tough, stipitate, surface of pileus and stipe distinctly rough-scaled, tubes long, regular, even, not easily separated from the pileus; spores dark brown, netted.

One species in Iowa.

1. *S. strobilaceus* Berk.

Fig. 77

Pileus hemispherical to convex, surface roughened by thick cone-like projecting blackish or blackish-brown scales, dry, soft and spongy; margin fringed with scales and fragments of veil, 3-10 cm. broad; context white or grayish-white, changing to red and then blackish when wounded, taste mild; tubes adnate, whitish, becoming brown or blackish with age, mouths large, angular, changing color like the context, blackish on drying; stipe equal or slightly tapering upward, striate when it joins the tubes, floccose tomentose, color of pileus, solid, 3-12 cm. long, 1-2 cm. thick; spores subglobose, rough, blackish-brown, under oil immersion lens distinctly netted, 10-12 μ ; veil dense, cottony, white to grayish, adhering to margin and stipe when mature.

Genus *BOLETUS* Dill. ex Fr.

Sporophore fleshy, putrescent, stipe central; hymenophore composed of long or short tubes, free from stipe, or decurrent, round or angular, easily separable from the context of the pileus and from each other; terrestrial, annual; cystidia sometimes present, spores variously colored.

The genus includes many species, and is separated from *Polyporus* by the absence of a trama descending from the context into the tubes; from *Boletinus* by the tubes being easily separated from the pileus.

The study of *Boletus* has been based very largely on dried specimens in the Mycological Herbarium of the State University of Iowa. Since dried specimens of *Boletus* are very difficult to identify some of the species reported may be open to question. This seems to be the first attempt to classify the *Boletes* of Iowa. There are undoubtedly many other species represented in the state, but only those which were available for careful study are included here.

KEY TO THE SPECIES OF *BOLETUS*

- a. Context white at maturity -----b
- a. Context not white at maturity -----m
 - b. Stipe not at all reticulate with veins -----c
 - b. Stipe reticulate with veins -----j
- c. Stipe scabrous or punctate-squamulose -----1. *B. scaber*

- c. Stipe not scabrous or punctate -----d
 - d. Pileus and stipe black or blackish -----2. *B. nigrellus*
 - d. Pileus and stipe not black when fresh -----e
- e. Pileus with a thin separable cuticle which easily cracks and rubs off in spots, stipe spongy and white within, sometimes slightly reticulate at base -----3. *B. affinis*
- e. Pileus not as above -----f
 - f. Stipe spongy within, soon cavernous or hollow, pileus minutely velvety tomentose -----4. *B. castaneus*
 - f. Stipe solid -----g
- g. Tubes and context unchanging, pileus tomentose, tubes yellowish, large angular -----5. *B. subtomentosus*
- g. Tubes and context changing to blue when wounded -----h
 - h. Pileus and stipe glabrous -----6. *B. pallidus*
 - h. Pileus usually tomentose -----i
- i. Tubes yellow and large, pileus and stipe usually red, often cracked -----7. *B. chrysenteron*
- i. Tubes at first grayish-white, discolored later by the spores, pileus distinctly reticulate rimose -----8. *B. fumosipes*
 - j. Tubes becoming flesh colored -----k
 - j. Tubes becoming yellow or greenish yellow -----l
- k. Taste mild, pileus some shade of yellow or brown -----9. *B. indecisis*
- k. Taste bitter -----10. *B. felleus*
 - l. Pileus glabrous, or very finely tomentose -----11. *B. edulis*
 - l. Pileus not glabrous, squamulose or punctate, reticulate at base -----12. *B. variipes*
- m. Stipe with an annulus -----n
- m. Stipe without an annulus -----o
 - n. Spores globose or subglobose -----13. *B. sphaerosporus*
 - n. Spores oblong-ellipsoid -----14. *B. Clintonianus*
- o. Stipe shaggy and scabrous -----p
- o. Stipe smooth or reticulate -----q
 - p. Stipe shaggy and lacerated with reticulate folds; pileus dry, tomentose -----15. *B. Russelhi*
 - p. Stipe scabrous and pileus glabrous, slightly viscid -----1. *B. scaber*
- q. Tubes yellowish with reddish or reddish-brown mouths -----16. *B. luridus*
- q. Tubes of one color -----r
 - r. Tubes nearly free, stuffed when young -----11. *B. edulis*
 - r. Tubes adnate, not stuffed when young -----s
- s. Stipe reticulate with veins -----t
- s. Stipe not reticulate with veins -----u
 - t. Context and tubes changing to blue where wounded -----17. *B. speciosus*
 - t. Context and tubes not changing to blue where wounded -----18. *B. ornaticipes*
- u. Pileus viscid or gelatinous when moist, tubes glandular dotted -----19. *B. americanus*

- u. Pileus dry -----v
- v. Tubes not changing to blue when wounded--5. *B. subtomentosus*
- v. Tubes changing to blue when wounded -----w
- w. Context reddish beneath the cuticle -----7. *B. chrysenteron*
- w. Context not reddish beneath the cuticle -----x
- x. Stipe yellow, sometimes with red stains.20. *B. miniata-olivaceus*
- x. Stipe red, yellow at top -----21. *B. bicolor*

1. *B. scaber* Bull. ex Fr.

Fig. 78

Pileus thick, fleshy, convex, glabrous or minutely tomentose, slightly viscid when fresh or when moistened after being dried, varying in color from white to brownish or reddish, margin thick; context white or whitish, darkening when bruised, taste mild; tubes free or nearly so, remote from stipe, mouths convex, small, round, long, white becoming brown when dry, darkening when bruised; stipe solid, attenuate above, whitish especially above, brownish below, scabrous or roughened with small reddish or blackish or brownish dots or scales, not reticulate, 5-15 cm. long, 1-1.5 cm. thick; spores yellowish-brown, smooth, oblong-fusiform, 10-17 x 4-6 μ ; hyphae of context a hyaline reticulate network.

Syn. *Ceratomyces viscidus* (L.) Murrill.

2. *B. nigrellus* Pk.

Fig. 79

Pileus convex or nearly plane, dry, pruinose to finely tomentose, very dark brown to black, margin involute, rather thick, 6-14 cm. broad, 2 cm. thick; context white changing to pinkish gray when dry, taste nutty; tubes adnate, plane or convex, depressed around stipe, 1 cm. long, mouths small, subcircular, pale-gray to flesh-color, changing to black or brown when wounded; stipe solid, subequal, 5-8 cm. long, 1.5-3 cm. thick, concolorous or a little paler than the pileus, velvety at the base, not reticulate; spores greenish to dull flesh colored, smooth, oblong-ellipsoid, epiculate, 8-11 x 4-5 μ .

Syn. *Tylophilus alboater* (Schw.) Murrill.

3. *B. affinis* Pk.

Pileus convex to plane, dry, glabrous or minutely tomentose, slightly viscid when moist, usually dry, brown or chestnut color, fading to tawny or ochraceous with age, sometimes

rimose-areolate or spotted, 5-10 cm. broad; context somewhat spongy, white, sometimes changing to yellowish where wounded; tubes adnate or nearly free, plane or convex, at first white and stuffed, then yellow or subferruginous when wounded, 2-3 per mm.; stipe unequal, narrowed either above or below, even or rarely reticulate at the top, glabrous, colored like or paler than the pileus, spongy within, sometimes tinged with red, 4-9 cm. long, 8-16 mm. thick; spores bright ferruginous-ochraceous, 9-12 x 4-5 μ .

Syn. *Boletus crassipes* Peck.

This species was reported by H. W. Paige, as occurring near Fort Dodge, Iowa, in August.

4. *B. castaneus* Bull. ex Fr.

Fig. 80

Pileus firm, dry, convex, plane or depressed, later expanded, minutely or velvety tomentose, cinnamon, reddish brown or chestnut colored, margin thin, 3-7 cm. broad; context white, unchanging when bruised, nutty odor; tubes free, short, small, white becoming yellow to brown when dried; stipe loosely stuffed, later becoming hollow, equal or tapering upward, cylindrical, tomentose and concolorous with pileus, not reticulate, 3-5 cm. long, 6-10 mm. thick; spores hyaline to pale-yellow, yellow in mass, smooth, oval or ellipsoid, with an oblique epiculus, 8-10 x 4.5-6 μ ; in late summer; fairly common.

Syn. *Gyroporus castaneus* (Bull.) Quel.

5. *B. subtomentosus* Linn. ex Fr.

Fig. 81

Pileus soft, dry, convex to plane, villose-tomentose, often rimose-areolate, yellow in chinks where cracked, yellowish brown, reddish-brown or tawny, margin entire, involute when young; 2-10 cm. broad; context white or yellowish, unchanging, taste mild; tubes adnate, slightly decurrent, dull yellowish, unchanging, mouths large, angular, irregular, elongated near stipe; stipe solid, equal, expanded above or tapering below, yellow, sometimes sulcately ribbed, nearly covered with straight red lines, not reticulated, scurfy with minute dots, yellowish within, 3-9 cm. long, 7-18 mm. thick at top; spores snuff brown in mass, brownish or greenish yellow under micro-

scope, smooth, subfusiform $11-14 \times 4-5 \mu$; solitary or gregarious; on ground or humus of stumps; a common and variable species.

6. *B. pallidus* Frost.

Fig. 82

Pileus soft, dry, convex, becoming plane or depressed, glabrous, pallid or brownish-white, slightly tinged with red, margin even, rather thin, fertile, 5-10 cm. broad; context white, becoming bluish when wounded; tubes nearly adnate, plane or slightly depressed, pale or whitish-yellow, becoming dark-flavous with age, changing to blue when wounded, mouths small, angular; stipe solid, equal or thickened at the base, glabrous, not reticulated, whitish often streaked with brown or red, often tinged with red within, 6-15 cm. long, 7-15 mm. thick; spores pale ochraceous brown, smooth, oblong-ellipsoid, $8-12 \times 4-5 \mu$.

7. *B. chrysenteron* Fr.

Fig. 85

Pileus convex to expanded, sometimes depressed, surface dry, tomentose to floccose-squamulose, often rimose-areolate, variable in color, some shade of red or purple or cinnamon, especially when older, brown, margin entire, fertile, 4-8 cm. broad, 1-2 cm. thick; context yellowish-white to flavous, reddish beneath cuticle, quickly changing to blue or greenish when wounded, taste mild; tubes adnate, convex in mass, slightly decurrent, becoming much depressed when old, yellow or greenish yellow within, changing like the context when wounded, mouths wax yellow, large, angular, irregular, 1-2 per mm.; stipe solid, subcylindric, tapering at base, red or reddish streaked below, flavous, longitudinally furrowed, glabrous or minutely scurfy or longitudinally furrowed, cortex yellowish within at the base, changing to blue, 3-8 cm. long, 0.3-1.5 cm. thick, not reticulate; spores olivaceous when fresh, fading to pale brownish, smooth, fusiform, $12-14 \times 4-5.5 \mu$; cystidia brown, 10-35 μ , numerous, projecting 10-20 μ .

Syn. *Ceratomyces communis* (Bull.) Murrill.

8. *B. fumosipes* (Peck) Murrill

Fig. 86

Pileus convex or plane, minutely tomentose, distinctly reticu-

late-rimose, avellaneous to umbrinous or dark-olive brown; margin entire, fertile, 4-7 cm. broad, about 1-1.5 cm. thick; context white, changing slowly and slightly to pale-blue or bluish green, firm, fleshy, taste mild or sweet; tubes plane, convex when older, as long or longer than thickness of context, greenish-white to avellaneous; stipe solid, equal, somewhat ventricose, minutely scurfy, 3-5 cm. long, 0.7-1 cm. thick, avellaneous-umbrinous to fulvous, paler above, paler bluish-green at the apex, not reticulate, dirty white within; spores deep ochraceous brown, cylindric or fusoidsigmoid, smooth, $8-12 \times 4-5.5 \mu$; these spores are not as large as reported by Murrill. He reports them as $14-16 \times 7-8 \mu$. The species is probably of doubtful occurrence and should be studied more carefully from fresh material.

Syn. *Ceromyces fumosipes* Pk.

9. *B. indecisis* Pk.

Fig. 87

Pileus thick, dry, convex or nearly plane, slightly tomentose or velvety to glabrous, ochraceous-brown to chestnut, margin entire to wavy, 6-12 cm. broad; context white, firm fleshy, unchangeable, 0.3-1.5 cm. thick; taste mild or sweet; tubes adnate, usually plane, white or grayish, changing to brownish where bruised and when dry, mouths small, subcircular, 0.5-1.5 cm. long; stipe solid, concolorous, surface usually reticulated above and furfuraceous especially below, 6-10 cm. long, 1-2 cm. thick; spores brownish flesh-color in mass, smooth, oblong, $10-15 \times 4 \mu$.

10. *B. felleus* Fr.

Fig. 88

Pileus thick, soft, convex to nearly plane, glabrous, even, variable in color, usually some shade of tan or chestnut, or pale-yellowish to grayish-brown, often changing to flesh color when wounded, 8-15 cm. broad or larger; context white, often changing, flesh-color or pinkish when wounded, taste bitter when fresh, also when dry; tubes adnate, convex, depressed around stem, 0.5-2 cm. long, mouths angular, white becoming flesh-color or darker with maturity of spores; stipe solid, cylindric, equal or tapering upward, sometimes bulbous at the

base, glabrous, usually reticulate above, sometimes to base, 5-12 cm. long, 1 cm. or more thick; spores flesh-colored, smooth, oblong-fusiform, 10-15 x 3-4 μ . Common.

11. *B. edulis* Bull. ex Fr.

Fig. 89

Pileus thick, moist, convex or nearly plane, glabrous, or finely tomentose, at first compact, then soft, grayish-red, reddish-brown, tawny-brown or paler; margin acute or blunt, entire, 7.5-15 cm. broad; context white or yellowish unchanging, sometimes pinkish or reddish tinged beneath cuticle, taste and smell sweet and nutty; tubes semi-free, convex, nearly plane, white, then yellow and greenish, long, mouths small, angular or round; stipe solid, short or long, enlarged at base, stout, more or less reticulate, especially above, whitish pallid or brownish, 5-15 cm. long, 1.5-3 cm. thick; spores greenish-yellow to ochraceous brown, smooth, oblong-fusiform, 11-15 x 4-5 μ ; 1-3 guttulate. This species varies considerably in the size, color, and character of the stipe. Var. *clavipes*—Stipe tapering upward from an enlarged base.

Syn. *Boletus separans* Peck; *Ceromyces crassus* Batt.

12. *B. variipes* Pk.

Pileus thick, soft, dry, convex to plane, squamulose punctate, or minutely tomentose, grayish or pale-grayish brown, sometimes tinged with yellow or ochraceous; context white, unchanging, sweetish not bitter; tubes nearly plane, slightly depressed around stipe, at first white, then greenish-yellow, mouths small, subrotund, ochraceous, stuffed when young; stipe firm, whitish or pallid, reticulated, variously shaped, often enlarged at base; spores ochraceous brown or tinged with green, smooth, oblong-fusiform, 12-15 x 5 μ .

13. *B. sphaerosporus* Pk.

Fig. 90

Pileus hemispherical, convex, with a veil covering tubes underneath, glabrous viscid, creamy-yellow when young, changing to reddish brown or chestnut color, margin thin, even, often inflexed when dry, 3-15 cm. broad; context pale yellowish-brown, becoming brown when dry; tubes adnate,

slightly decurrent, pale-yellow changing to brown when bruised or olivaceous from spores, edges thin, mouths large, angular, uneven, some elongated into coarse teeth; stipe solid, stout, thick, equal, glabrous, reticulate at apex at least not more than half way down, annulus persistent, sometimes adhering to margin of pileus, 1.5-3 cm. thick, 3-7 cm. long; spores yellowish-brown, smooth, globose to broadly elliptical 5-10 μ , variable in size. Fairly common.

14. *B. Clintonianus* Pk.

Fig. 91

Pileus convex, gregarious, viscid, glabrous, with separable cuticle, golden yellow to chestnut color, margin at first incurved, then thin and spreading; context pale yellow, or golden yellow, becoming less bright or slightly greenish when wounded, taste mild; tubes adnate or subdecurrent, nearly plane, small, pale yellow to dingy ochraceous with age, changing to reddish or purplish-brown when bruised; stipe annulate, subequal, slightly thickened at base, straight or flexuous, yellow at the top, reddish or reddish-brown below annulus, annulus white or yellow, persistent, rather thick; spores brownish-ochraceous, oblong, 10-12 x 4-5 μ .

Shaded grassy places, in woods or open places.

15. *B. Russellii* Frost

Fig. 94

Pileus thick, convex, dry or slightly viscid when moist, tomentose-squamulose, or tomentum agglutinated in raised squamules, appearing somewhat reticulate or rimose areolate, drab gray, yellowish beneath tomentum, 3-10 cm. broad; context yellowish or tan, unchanging, taste mild, salty, 1-2 mm. thick; tubes adnate to subdecurrent, plane or convex, often depressed around stipe, dingy-yellow, yellowish-green, or dark flavous with tinge of green at maturity, mouths large, angular, edges thin; stipe long and slender, equal or tapering upward, very coarsely reticulate and fluted, roughened by lacerated margins of reticular depressions, glutinous, red or brownish-red, yellow within, 5-12 cm. long, 1-1.5 cm. thick at base; spores olivaceous, smooth, ellipsoid, distinctly longitudinally striated, 13-17 x 8-10 μ .

16. *B. luridus* Schaeff. ex Fr.

Fig. 95

Pileus dry, convex, somewhat viscose, glabrous, minutely tomentose or rimose areolate, brown with red-yellow shades chestnut to auburn, 5-10 cm. broad, margin thick, obtuse, entire; context yellowish, turning to blue when wounded; tubes free or nearly so, plane or slightly depressed, yellow, becoming greenish blue when wounded, mouths small, circular, cinabar red to orange, darker with age; stipe solid, equal or tapering upward, red, dark-reddish within, reticulate or punctate, red or reddish brown below, 4-8 cm. long; spores greenish-gray, smooth, $9-12 \times 4-8 \mu$, variable in size, cystidia present, $15-20 \times 8-10 \mu$, yellowish-brown.

17. *B. speciosus* Frost

Pileus at first thick, subglobose to convex, glabrous or subglabrous, smooth, slightly moist, red; context firm, taste nutty, pale or bright lemon-yellow, changing to greenish-blue when wounded; tubes adnate, small, subrounded, plane or slightly depressed, bright yellow, becoming dingy with age, changing like the context; stipe stout, unequal, solid, reticulate, bright lemon-yellow within and without, or reddish at base, 5-10 cm. long, 2-5 mm. thick; spores pale ochraceous-brown, oblong-fusiform, $10-12 \times 4-5 \mu$.

In woods.

18. *B. ornatipes* Pk.

Fig. 96

Pileus dry, or very slightly viscid when wet, convex, becoming plane or somewhat depressed, glabrous or finely tomentose, sometimes minutely rimose-areolate, reticulate in appearance, avellaneous, clay colored or isabelline, often greenish in center, 5-14 cm. broad, 2-4 cm. thick; context yellowish, unchanging; taste mild or slightly salty; tubes adnate, slightly decurrent, somewhat depressed with age, lemon-yellow when young becoming dull yellow and dark brown when dried, mouths circular to angular, dissepiments thin, 1 cm. or more long; stipe rarely caespitose, firm in outer portion, sometimes becoming spongy within, subequal, often bulbous at base, distinctly and beautifully reticulate, the bottom of

the reticulate chambers buff yellow, the ridges hazel, 5-12 cm. long, 0.5-2 cm. thick; spores olivaceous, or greenish-ochraceous, snuff-brown in mass, smooth, 10-14 x 3-4.5 μ ; cystidia brown and hyaline, 20-35 x 7-12 μ .

Syn. *Ceriomycetes retipes* (Berk. and Curt.) Murrill.

19. *Boletus americanus* Peck

Fig. 97

Pileus thin, soft, convex to nearly plane, surface yellow, viscid when moist, slightly tomentose on margin when young, otherwise glabrous, sometimes gray-spotted from drying of gluten, 2.5-7 cm. broad; context pale-yellow, pinkish-gray when wounded, taste mild, 2-5 mm. thick; tubes adnate, hardly decurrent, mouths rather large, angular, yellow to dull ochraceous when dry, covered by glandular dots; stipe solid, equal or slightly tapering toward the top, brown or reddish-brown, glandular dots on surface in fresh and dried specimens; 3-6 cm. long; spores ochraceo-ferruginous, smooth, 8-12 x 4-5 μ .

Syn. *Rostkovites subaureus* (Peck) Murrill.

20. *B. miniato-olivaceus* Frost

Fig. 83

Pileus firm to somewhat soft and spongy with age, convex to plane, glabrous or finely tomentose, sometimes rimose areolate, vermilion changing to olivaceous or ochraceous with age, changing blue when wounded, margin acute or slightly exceeding the pores; context pale yellow, changing to blue when wounded, mild or slightly unpleasant taste; tubes adnate or subdecurrent, slightly depressed, bright lemon-yellow tinged with green becoming brownish-yellow with age, changing to blue when wounded, mouths subangular of medium size; stipe solid, equal, or enlarged above or below, pale-yellow with pink markings especially at base; yellowish within, faintly reticulate at the top, 6-10 cm. long, 5-1.5 cm. thick; spores yellowish-brown, smooth, oblong-ellipsoid, 10-13 x 4-5.5 μ .

Syn. *B. glabellus* Peck.

B. miniato-olivaceus seems to be very similar to *subtomentosus*. According to Murrill and Peck it differs mainly in its context and tubes changing to blue wherever bruised or cut.

There is one specimen so labeled in the State University of Iowa Herbarium.

21. *B. bicolor* Pk.

Fig. 84

Pileus somewhat irregular, firm becoming soft, convex, glabrous, finely tomentose or squamulose, at times rimose-areolate with age, dark red or purplish-red, often becoming paler and spotted with yellow when old, margin irregular; context yellow, usually changing very slightly to blue when wounded, taste mild; tubes adnate, short, nearly plane, yellow, becoming ochraceous with age, changing to blue or greenish-blue when wounded, mouths medium sized, angular, 2-3 per mm.; stipe solid, equal or nearly equal, firm, nearly glabrous with a few dark dots showing under hand lens, red except at the top, where it is yellow and slightly reticulate, flavous within, usually slowly changing to blue, 4-10 cm. long, 7-1.5 cm. thick; spores pale ochraceous-brown, smooth, fusiform, 11-15 x 4-6 μ ; cystidia yellowish-brown, projecting 20 μ , 3-5 μ broad, August to October.

Genus *BOLETINUS* Kalchbr.

Sporophore fleshy or spongy; annual, terrestrial or epixyloous; context whitish or yellowish; hymenophore composed of broad radiating shallow lamellae connected by very numerous more narrow anastomosing branches or partitions, and forming large angular pores; not easily separable, adnate or slightly decurrent.

Only one species is represented in Iowa.

B. porosus (Berk.) Pk.

Fig. 92

Pileus fleshy, reddish-brown, yellowish-brown, or umber, dry or when moist, viscid, shining, margin thin and even, 3-10 cm. broad; context 5-20 mm. thick; tubes yellow, short, formed by radiating lamellae branching and connecting by numerous irregular veins of less prominence and forming large angular pores; stipe lateral or eccentric, tough, diffused with the pileus, reticulate at the top by the decurrent walls of tubes concolorous with pileus; spores hyaline or yellow, smooth, ovate or semi-ovate, 7-8 x 5-7 μ .

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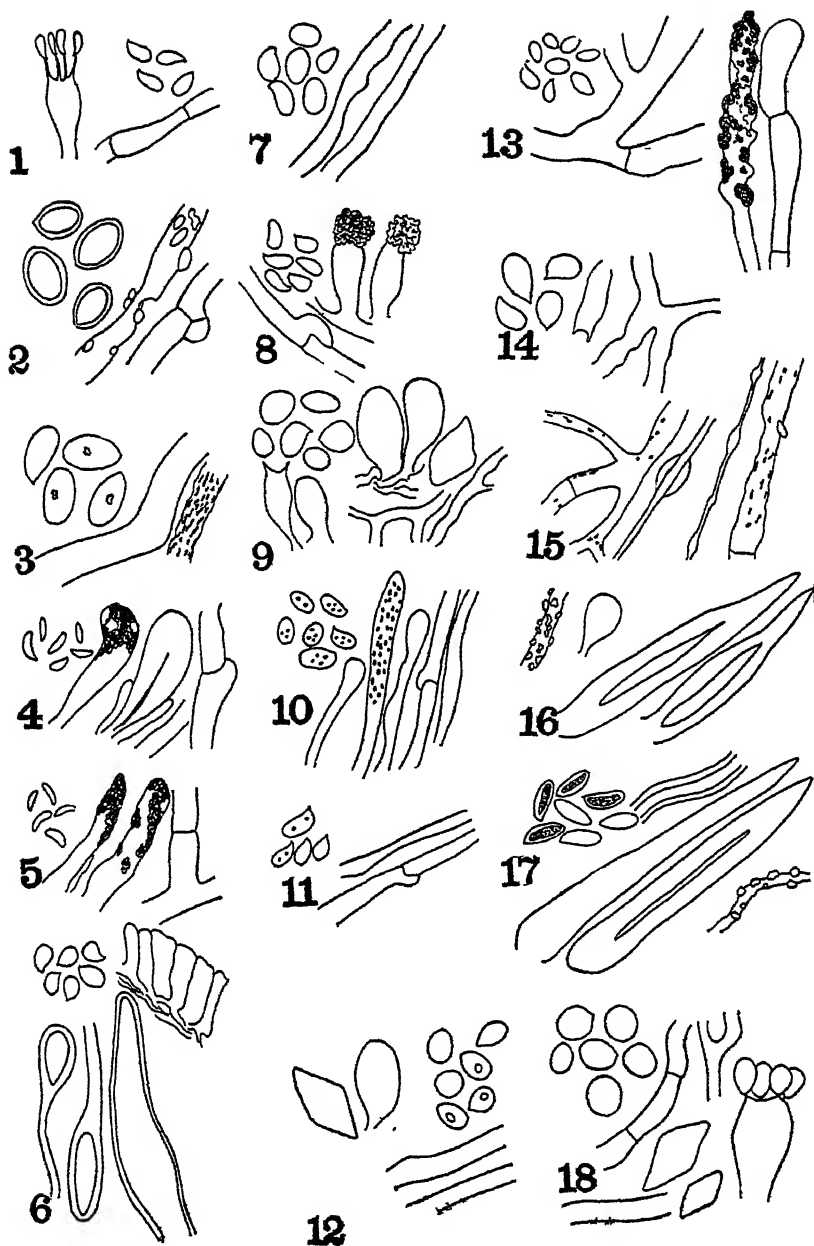


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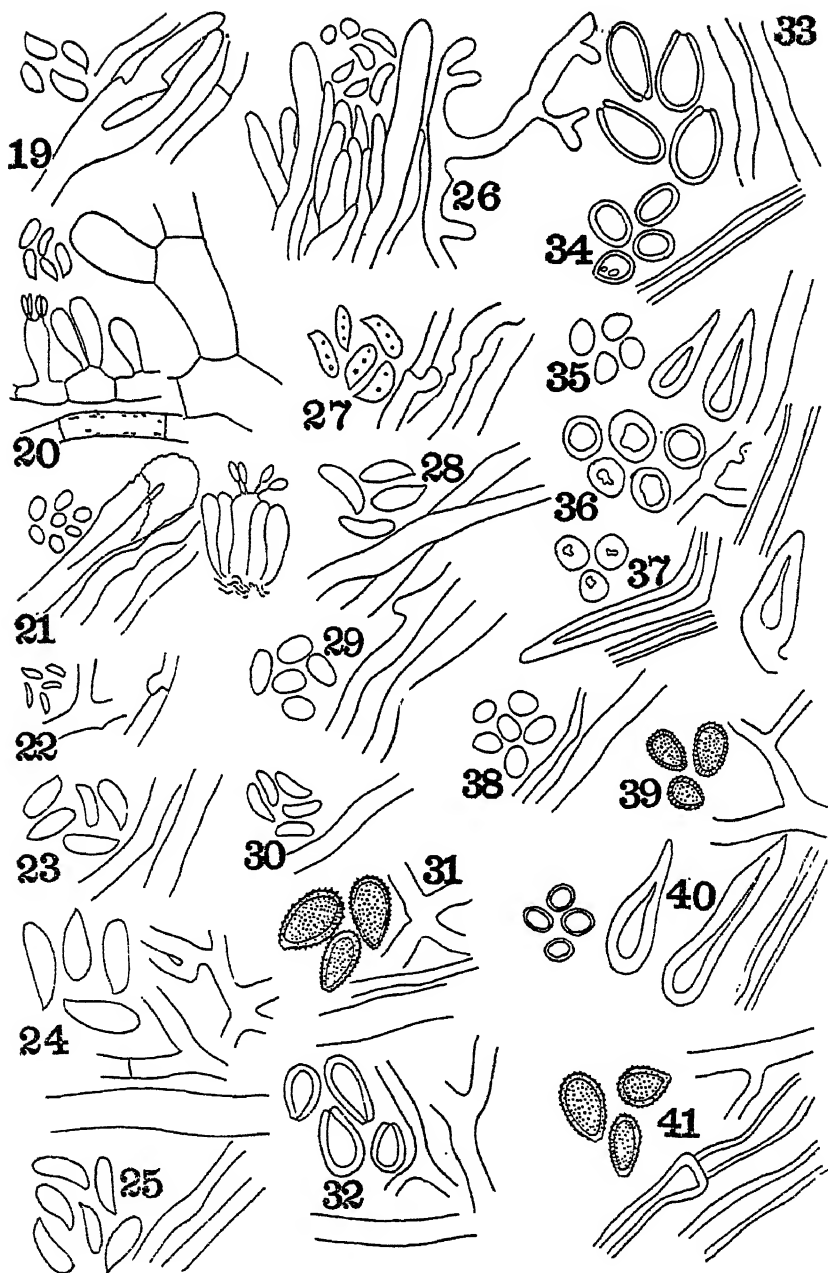


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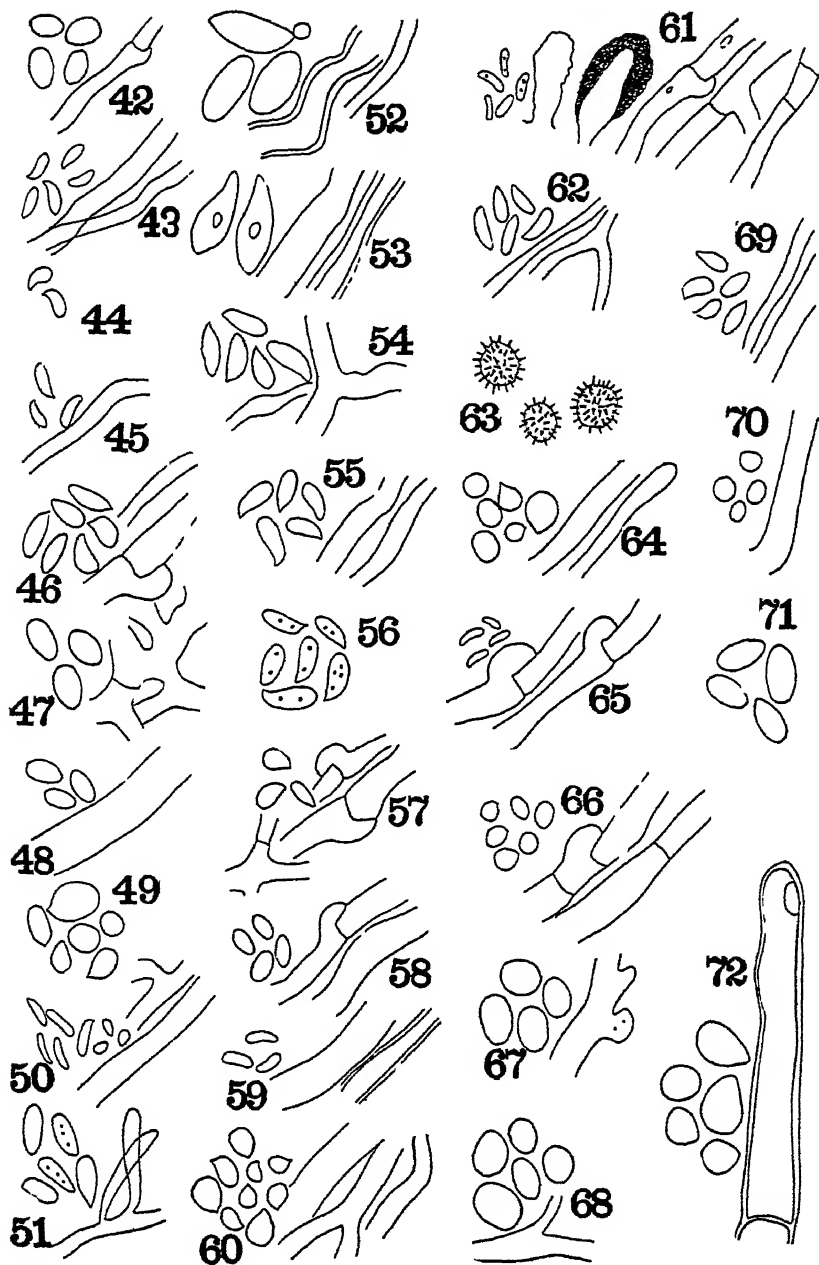
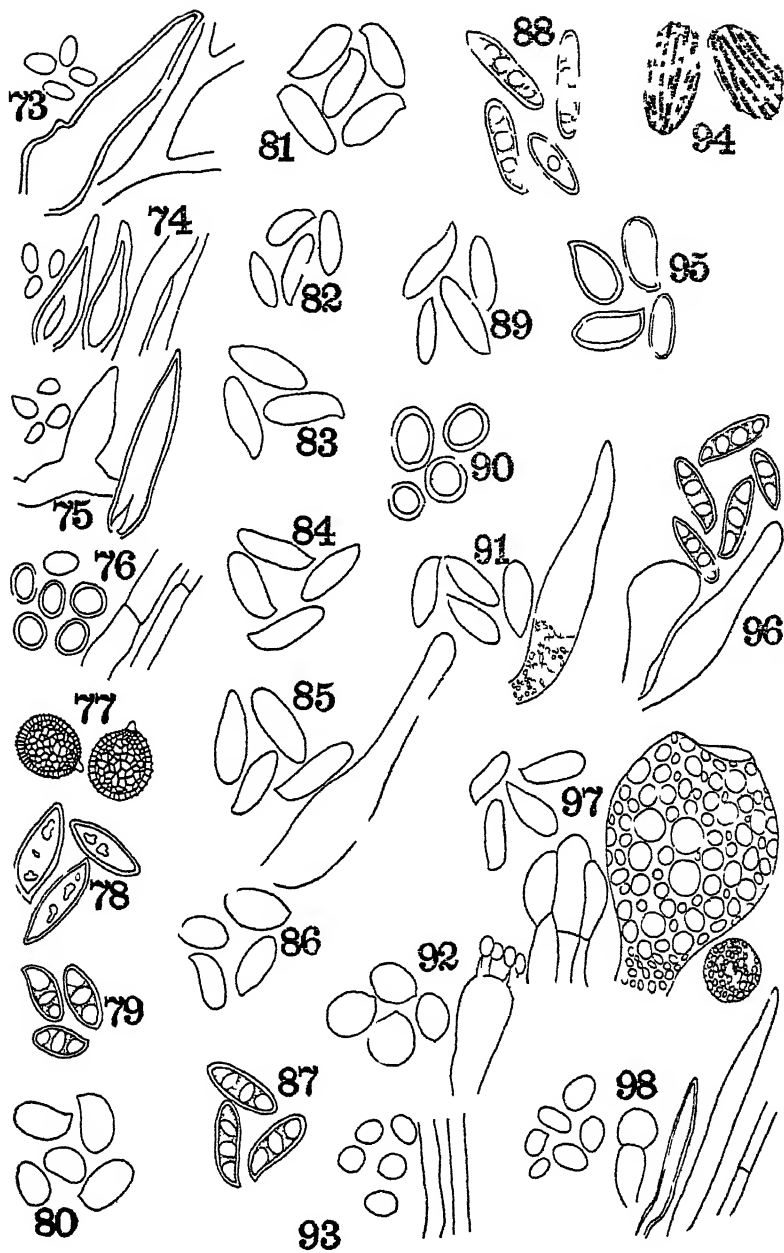


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MISCELLANEOUS PAPERS

by

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COMMON NAMES OF PLANTS

B. SHIMEK

The discussion of the use of common names for plants has been less intense among professional botanists than that of rules of nomenclature for scientific names. The question, however, is of interest not only to the amateur lover of plants, but to the botanist as well.

The scientific name is, of course, more accurate, more widely used in fairly consistent fashion, and it should be employed in all scientific records, and in all other cases requiring accuracy, as, for example, in noxious-weed laws, tree-planting laws, etc.

Objections to scientific names on the score that they are too difficult, so often made by amateurs, lose much of their weight when we consider that many scientific names, such as *Chrysanthemum*, *Gladiolus*, *Clematis*, *Asparagus*, *Trillium*, *Amaryllis*, etc., are in common use as vernacular names; and that a number of scientific names, such as *Nasturtium*, *Geranium*, *Smilax*, *Calla*, etc., are improperly used as common names. Surely it would be as easy to use the latter names correctly as it is to use them incorrectly!

Despite the fact that scientific names are more consistent, more accurate, and often more expressive, common names are, and will continue to be, very widely used. Their greatest weakness is that they cannot be used internationally. Other weaknesses, such as lack of standardization, could be remedied in time by agreement and by education.

Those who are untrained in botanical lore find common names much more usable. With the increased attention to the outdoor world by organizations of various kinds, and with the back-to-nature tendency which is greatly stimulated by the increasing number of state and national parks toward which great numbers of visitors gravitate each year, there is greater demand for knowledge of the identity of our plants. Mani-

festly scientific names would be of little interest to the untrained outdoor visitors, and they would probably merely serve as barriers to that growing interest in plants which should especially be encouraged by botanists.

The teaching botanist will also find common names useful. While he should use scientific names for his own records and references he is often called upon to address many, even in his own classes, who have had no training in systematic botany, and he must use common names when he refers to specific plants if he is to be understood.

Too often this is necessary also when he addresses those who have had training in botany (and this often includes graduate students), but who have not learned how to identify the materials with which they work. The remedy for this type lies, of course, in presenting this phase of the work to the student early in his career, and not, as is now so often done, when he is approaching the end of his scholastic preparation,—if at all! There is, unfortunately, a widely prevalent and wholly erroneous notion, chiefly among those whose experience in this field is limited, that taxonomic work can be undertaken only by advanced students, when as a matter of fact it should be presented in the high school.

Laymen and botanists alike have use for common names, but this does not mean that they should permit them to supplant scientific names to any important extent, especially so long as the vernacular nomenclature is in its present chaotic state.

This confusion in common names arises from several causes, some of which are here briefly noted.

Local names have developed in all parts of the country, and of the world. Sometimes they were suggested by economic and other uses, again by habits, size, color, or other characteristics, or by resemblance to some other plant, thus bringing about a great diversity of local names, often for the same species.

The confusion was not infrequently augmented by transferring the name of a plant of one locality or country to that of another because of some fancied resemblance, or some common use.

This multiplicity of names has been perpetuated by the publication of the various names in manuals, descriptive accounts and lists, and frequently several names have thus been placed on record for the same species. In most cases a more or less conservative effort has been made to limit the number of such names in each publication, but unfortunately the authors have not always used the same names, and the confusion continues.

Thus, for example, Britton's Manual designates *Larix laricina* as Tamarack, Hackmatack, or American Larch, and Gray's Manual adds Black Larch to the foregoing.

Gray's Manual calls *Prunus pennsylvanica* Wild Red Cherry, Bird Cherry, Fire Cherry or Pin Cherry, and Britton's Manual adds Pigeon Cherry.

In Harriet L. Keeler's "Our Native Trees," one of the better popular tree manuals, 54 of the 139 species described have but one name each, while 85 have two to four names.

In Sargent's more comprehensive "Manual of the Trees of North America," 291 species have but one common name each; 162 have two each; 2 have three each; 2 have a common name for the genus only; and 175 are without common names.

Much greater confusion arises, however, from the use of the same common name for different species.

In Gray's Manual each of 48 common names is applied to more than one species, 41 being used for two species (in 9 cases belonging to the same genera, and in 32 cases to different genera), and 7 for three species in part belonging to different genera. In some cases the species designated by the same name are widely separated in relationship, as for example, Black Snakeroot (*Cimicifuga racemosa* and *Sanicula*), Fireweed (*Epilobium angustifolium* and *Erechtites*), Goat's-beard (*Arun-cus* and *Tragopogon*), Wild Liquorice (*Glycyrrhiza lepidota* and *Galium circaezans*), Richweed (*Pilea* and *Collinsonia canadensis*), Button Snakeroot (*Eryngium yuccifolium* and *Liatris*), Starwort (*Stellaria* and *Aster*), Blazing Star (*Chamaelirium luteum* and *Liatris*), and Goose-grass (*Eleusine*, *Puccinella maritima* and *Galium aparine*).

No reference is here made to the numerous names which differ only in their qualifying adjectives. These are more numerous in Britton's Manual than in Gray, with some cor-

responding diminution in the number of names exactly duplicated. Of the latter, however, Britton uses 30, of which only two, Wild Madder and Post Oak, are applied in each case to two species of the same genus. In all the other cases the same name is applied to species of different genera. In most cases two genera are thus represented, and in the main they are not closely related, the extreme, perhaps, being reached in the application of the name Hemlock (without adjectives) to species of *Tsuga* and *Oxyopsis*. In two cases, those of the Rattle-box and Wire-grass, representatives of three genera are included under the same common name.

Because of their economic value and the popular interest which they have always aroused, trees have suffered from multiplicity of names more than any other group of plants.

In the very conservative "Our Native Trees," previously mentioned, only 10 common names are exactly duplicated, 8 being applied to members of the same genus, and 2 to members of different genera.

In Sargent's "Manual of the Trees of North America" the same common name is applied to two or more species of the same genus in 64 cases, 39 being applied to two species, 13 to three species, 9 to four species, and 1 each to five, seven and eight species. Thus, 4 species of *Malus* are called Crab-apple; 4 of *Salix*, Black Willow; 5 of *Populus*, Cottonwood; 4 of *Acer*, Sugar Maple; 8 of *Yucca*, Spanish Dagger; in *Pinus*, 4 as Nut Pine or Pinon, and 4 as Yellow Pine; in *Quercus*, 4 as Black Oak, 4 as Live Oak, 4 as Scrub Oak, and 7 as White Oak; while the name Red Fir is applied to one species of *Pseudotsuga* and three of *Abies*; the name Iron-wood to one species of *Cyrilla* and three of *Ostrya*; and the name Hemlock to one species of *Pseudotsuga* and four of *Tsuga*. In ten other cases species belonging to different genera are designated by the same common name.

One unfortunate feature of certain common names which have been coined in recent time is their inconvenient length resulting from an effort to make them descriptive. Such names as "Narrow-leaved White-topped Aster," and "Filiform White Water-crowfoot" are cumbersome and seem to carry us back in nomenclature to pre-Linnean times.

The attempt to express fancied resemblances in some cases,

and possibly carelessness in others, have resulted in the use of misleading names. Thus we have several species of true oaks, and in addition to that the Jerusalem Oak and Poison Oak are recognized, but neither is related to the oaks; Prickly Ash and Mountain Ash are not related to the true ashes; the Blue Beech is not a beech; the Ground Hemlock is not a hemlock; the Dog's-tooth Violet is not a violet; the Prairie Wake Robin (*Trillium recurvatum*) does not grow on the prairies; and the Rockrose is neither a rose nor does it grow on the rocks. So far as possible such names should be eliminated.

The use of some common names, with adjective modifiers, for species not closely related is also a source of confusion. For example, we have "snake-roots" of various kinds in *Aristolochia*, *Cimicifuga*, *Psoralea*, and *Sanicula*, and also rattlesnake-"root," -"grass," -"master," and -"weed"; we have various nettles belonging to the genus *Urtica*, but we also have wood, false, dead, hedge, spurge, and hemp nettles which belong to other genera and even families; and the same is true of various lilies.

It is also unfortunate that our manuals, etc., perpetuate scientific names where used erroneously as common names. Such common names as Syringa, Smilax, Geranium, and Nasturtium should be eliminated.

Greater consistency should be observed in the use of common names. Sometimes a common name is given to a genus and its species receive common names which are wholly unrelated to it; group names are sometimes given to more than one genus, instead of restricting them to a genus, or subdivision of a genus; and very local names are sometimes published while those of much wider use are disregarded.

One of the difficult questions calling for settlement is that of common names for obscure species, or species in which specific differences are not conspicuous. Such genera as *Asplenium*, *Potamogeton*, *Rumex*, and *Salix* suggest illustrations. Often it is only a part of the genus which contains obscure forms, as in *Prunus*, *Ranunculus*, *Aster*, etc. Perhaps it would be best to adopt a group name (in many cases it might be the scientific generic name), and then indicate the species by numbers or letters. It would, for example, be much simpler

to write *Bidens a* instead of "Purple-stemmed Swamp Beggar-ticks."

Three methods of procedure suggest themselves in connection with the problem of the standardization of common names, and they are here briefly presented:

1. A check-list of common names should be prepared which will avoid, so far as possible, the weaknesses noted above. Vernacular nomenclature cannot follow ordinary rules of scientific nomenclature. No international considerations are involved; no law of priority can apply; no definite past date can be adopted as a starting point. The names in this check-list must be determined by agreement, particularly among all organizations interested in plant study, and when so determined they should be used in all subsequent publications.

2. Systematic botanists should participate freely in the work of the various clubs and organizations which are interested in outdoor life. Not only will they bring inspiration and information to places otherwise often inaccessible, but they will assist in broadening the field of influence of the standardized check-list.

3. More aggressive steps should be taken to restore systematic botany to its proper rank and place in the science curriculum. Certain phases of it should be presented in the secondary schools not only because of its value in developing systematic observation and thinking, but because the inevitable contact with the living world becomes a source of inspiration which will influence the entire lives of those who receive it early in their experience. If they do not go on with advanced botanical work they will have a source of wholesome physical, mental, and ethical influence throughout their lives, and if they do go on, their future work will be strongly influenced for the better by the inspiration and knowledge which they received. This work would offer perhaps the greatest opportunity for the establishment of the check-list as a standard for vernacular nomenclature.

This paper was read by request before the Systematic Section of the Botanical Society of America at the Cleveland meeting. The writer was not able to present it in person and hence could not press the adoption of the recommendation that a committee be appointed to coöperate with other similar

committees in the preparation of a check-list of common names. The recommendation is here repeated and urged upon all organizations interested in the vernacular nomenclature of our plants. Such work could be accomplished readily by correspondence and would entail little expense in connection with the preparation of the list.

THE RELATION BETWEEN THE MIGRANT AND NATIVE FLORA OF THE PRAIRIE REGION

B. SHIMEK

Even in a well established climax flora there is great fluctuation in the relative number of both individuals and species. The rapidity and character of these fluctuations is determined by various conditions.

We have, for example, the seasonal progression, repeated year after year, during which the flora displays very distinct and well-known phases.

Then there is the frequent fluctuation from year to year which is determined by the endless and extremely irregular variation in climatic and edaphic factors, each change favoring some forms, while others suffer.

And finally, there is the inevitable result of the accident of distribution in the uneven dispersal of seeds of the same species, due chiefly to changes in the direction and velocity of the wind, the volume and velocity of water currents, and the migrations and promiscuous wanderings of animals. In these cases the changes in the flora take place comparatively quickly in the case of annuals, and more slowly, though quite as effectively, in the case of perennials.

In this connection it is interesting to note that of the 265 species making up the bulk of the prairie flora of Iowa, 179 (67.5%) are ordinarily dispersed by wind; 65 (24.5%) by animals, chiefly birds; and 21 (8%) through hygroscopic properties.

The great majority of these species may also be dispersed more or less by surface water during heavy rainstorms, or by streams, especially when flooded. Violent tornadoes may also carry the heaviest of seeds and fruits.

The preponderance of wind-dispersed forms is significant, for during the summer months few days are quiet after the earlier morning hours. It also accounts for the fact that where a re-invasion of the prairie flora is taking place on areas which

had been disturbed, the wind-dispersed forms, particularly those which have capillary pappus, lead the invasion, and for a time usually take exclusive possession of the invaded area.

It is true, then, in a strict sense, that *all* the prairie flora is more or less migrant.

Ordinarily, however, we consider under that head the adventive flora which consists chiefly of what are usually designated as weeds.

This part of our flora is made up of two elements which are quite distinct in their source.

The great bulk consists of species which have been introduced from foreign lands, or from other parts of this country.

Cratty's recent list of the Immigrant Flora of Iowa contains 267 species. Of this number about 8 are widely distributed species which may have been introduced into some sections of our country, but appear to be native westward. The great majority of the others are found, some very locally, on cultivated grounds, or in the areas most completely dominated by man.

An interesting illustration of this fact is found in the distribution of this introduced flora in the vicinity of the towns of this state which are located on the older railways which were built before the prairie was broken. Along these railways belts of native prairie, usually varying from 10 to 20 feet in width, have been preserved, often for several miles, with only occasional interruptions by crossing highways, or where strips have been cultivated. Near the towns, however, there is invariably a strong weed element (often becoming dominant) which gradually fades out from the station, excepting on the roadbed proper, where it continues throughout. This distribution evidently results from the more frequent disturbances of the surface near the stations and along the roadbeds, and from the generous contributions brought in by railway trains, especially stock trains. These weeds do not enter the prairie strips on the sides of the railway right of way excepting where the surface has been disturbed.

In many cases these prairie strips have been preserved without appreciable deviation from the pure prairie type even where bordered on the one side by the roadbed with its ever

present belt of weeds, and on the other by farm lands which have been under cultivation for from thirty to sixty years.

Of the invaders from outside the state probably 20 have come from other parts of our country, chiefly west and south, while the great majority, nearly 240, were received from the Old World.

The greater part of this foreign flora usually takes possession of cultivated and otherwise disturbed open areas where it is quite certain to come in competition with the native flora of the prairies, particularly if cultivation (or other disturbance) is stopped.

Indeed this foreign flora is itself reinforced by a group of migrant native prairie plants which also occupy disturbed areas and mingle freely with the invaders, in some cases even crowding them into a subordinate place. This group includes such species as *Hordeum jubatum*, *Oxybaphus nyctagineus*, *Oenothera biennis*, *Asclepias syriaca*, *Convolvulus sepium*, *Verbena stricta*, *Solidago rigida*, *Erigeron ramosus*, *E. canadensis*, *Ambrosia artemisiifolia*, and more than 20 other less aggressive forms.

Along the railways both the foreign and native migrants mingle freely, and take quick possession of disturbed areas; but on prairie areas remote from the main lines of travel the native species take possession, to the complete or nearly complete exclusion of the foreign forms. They were evidently "weeds" even in the earlier history of the native prairie.

So thoroughly have these foreign and native species mingled and so widely have they been distributed, that some confusion exists as to the source of some of them. Among these may be mentioned *Equisetum arvense*, *Poa compressa*, *Hordeum jubatum*, *Amaranthus blitoides*, *Lepidium apetalum*, *Trifolium repens*, *Erigeron canadensis* and *Achillea millefolium* (including *A. lanulosa*).

While all the last-named species occur abundantly in cultivated fields, waste places, and along railways, they also occur freely on disturbed or rather barren prairie areas quite remote from the main lines of travel. This would suggest that these species are native, or that they were introduced long ago through other than human agency.

The published records of these species are decidedly confusing. For example, one author states that *Hordeum jubatum* occurs on prairies from Texas to Minnesota and westward; an-

other declares it came from west of the Missouri; while still another gives Europe as its source. *Lepidium apetalum* is given respectively as perhaps native in the western part of the United States; apparently naturalized from Asia; in the east introduced from Europe; and as occurring from Texas to Hudson Bay and westward. Other species of this group receive similar mistreatment.

As noted, this migrant flora usually takes quick advantage of any disturbance of the soil, for its members are the opportunists of the plant world. A gopher mound, an ant-hill, a newly eroded surface, an abandoned or neglected trail made by animals or man, and particularly the cultivation of large parts of the prairie, have furnished the conditions most favorable to invasion by this flora.

Man has contributed largely to the preparation of the surfaces for such invasion. His influence was no doubt felt long before the white man entered the prairies, for in the vicinity of their settlements and along the trails of their wandering bands, the aboriginal Indians not only constantly disturbed portions of the surface of the prairie but also aided in the transportation of migrant species.

Later, before the settlement of the prairie lands, wandering white hunters and trappers similarly aided in the distribution of the native migrant flora and occasionally introduced plant immigrants. This factor was by no means unimportant, for as late as the earlier eighties numerous hunters drove over the prairies of north-central Iowa in quest of game for the market as well as for sport.

This unstable element was soon followed by the actual settlers who not only disturbed the prairie by cultivation, but also introduced numerous foreign plant migrants with stock and crop seeds.

With the settlement of the country increased cultivation and improved methods of transportation still farther facilitated the introduction and diffusion of migrant forms. The railways especially contributed to this end. Not only did the construction and maintenance of the roadbed result in extensive and repeated disturbance of the prairie surface, but the trains brought in the seeds of many migrants.

An interesting comparative record is furnished by the Mani-

toba prairie. In 1883 and 1884 Christy found but three foreign weeds along the Canadian Pacific Railway between McGregor and Carberry. The railway was new, and the country was just being settled at the time. Thirty-six years later in the same territory the writer found forty species of Old World weeds, with a number of others that had probably been brought from the west.

In Iowa about 75 species of open-ground migrants have come to us from the Old World, and about one-half that number from other parts of the Western Hemisphere. About two-thirds of the foreign species have become more or less common.

Under certain conditions this introduced flora comes in direct conflict with the native prairie flora. As noted, areas which have been cultivated, or otherwise disturbed, are immediately invaded by a migrant flora, the major part of which is likely to consist of foreign forms, the remainder being made up almost wholly of the native "prairie weeds."

If cultivation is stopped, and the surface is not otherwise disturbed, there is gradual invasion of the area by species belonging to the more stable prairie flora, and the migrants are slowly crowded out, until finally the prairie flora is re-established. The rate at which the re-establishment takes place varies under different circumstances. Conditions under which plant growth is retarded usually rather favor the advance of the native prairie flora. During dry seasons, or on poor soils, for example, the native prairie flora has some advantage over the introduced migrants of the Old World, though the Russian Thistle forms an exception.

The availability of native seed for dispersal over the invaded area is also important. Where railways have been built through cultivated lands, for example, the restoration of the native flora on the undisturbed strips takes place very slowly and imperfectly, while in the cases in which strips of native prairie have been preserved along the railway right of way, or on uncultivated bits of prairie, the process is more rapid and more perfect. In a few cases which were followed rather closely by the writer the process required seven or eight years.

Contrary to a widespread belief the breaking up of the prairie turf does not permanently destroy the prairie flora,—it

will come back if given an opportunity,—i.e., if left undisturbed for several years, especially if remnants of the native flora have been preserved nearby.

Neither is it true that the matted roots of grasses are essential to the perpetuation of this turf. Extensive root systems characterize the prairie flora as a whole, and there were areas of large extent on which prairie plants other than grasses predominated. Moreover, in some cases which the writer has followed for a number of years the reinvasion of formerly disturbed areas was not accomplished first by grasses, but chiefly by Compositae with capillary pappus, such as *Solidago*, *Aster*, *Erigeron*, etc., which maintained their supremacy for years, without yielding noticeably to grasses.

The advance of the native prairie plants in such cases is not uniform. As a rule the perennials, which constitute more than 80 per cent of the prairie flora, advance more slowly, but persist better. The annuals and the few biennials, which make up the remainder, are more erratic. They frequently mingle with the introduced migrants from the first, and many of them, particularly the Ambrosias, *Erigerons*, *Hordeum jubatum*, *Oenothera biennis*, and others, form a very conspicuous part of the native "prairie weeds."

There is also a great difference in the persistence of the migrant forms, *Poa pratensis* among our American migrants, and *Melilotus* among the foreigners, probably being most tenacious. Even these forms, however, may be crowded out, or at least reduced to a very secondary position, by the native flora, though this is accomplished more slowly.

It is obvious that this whole problem is of great economic importance. Its relation to the weed-problem already has been briefly considered. Our weed-laws need severe revision, and they must particularly distinguish between our harmless prairie flora and the harmful migrants. Under the present indiscriminating practice we pave the way for the introduction of the objectionable migrants by destroying the native prairie flora which alone seems to be able to keep invaders out.

Some of our prairie remnants should be saved, and they may readily be enlarged from these remnants as seeding centers.

These areas should be saved not only that coming generations may enjoy something of the charm of primitive Iowa,

but because their study throws light upon the possibilities of plant-growing for economic purposes. The native flora represents the final outcome of the operation of all the ecological factors which have influenced plants through the centuries, and which are operating today not only on the remnants of the native flora, but on our crop plants as well.

For the purpose of preserving these records and these opportunities for study we should have well-selected prairie preserves in all parts of the prairie section of our country, each not less than a quarter-section in area.

Shall they be secured by private endowment? Shall they be sponsored by scientific societies? Shall the state and federal governments secure them? May railway companies be persuaded to preserve the prairie transects along their right of way? May our weed laws be so modified and interpreted that it will be possible to preserve strips of prairie flora along some of our highways rather than the noxious weeds which follow its destruction? These are questions for immediate consideration, before even these remnants of our prairie have disappeared.

Whatever may be the method, these areas should be secured, and there should be distinct limitations placed upon their uses. Landscape artists should be barred, and overzealous tree-planters should be restrained, in order that the *natural* prairie might be preserved; these preserves should not be made recreation grounds for picnickers and wandering tourists; their control should be placed in the hands of our educational institutions rather than our politicians; and portions of the tracts, particularly those which represent broken prairie, should be made experimental tracts under proper supervision by scientific workers representing every phase of the composite problem involved.

Our experience with the migrant flora teaches us that the prairie may be restored,—hence the prairie remnants may be enlarged to worthwhile dimensions. But this must be done before these remnants are totally destroyed. In Iowa such remnants are still found in all parts of the state, but each year they diminish in extent and number, and soon the prairie will be nothing but a vague tradition of a type even now forecast in some of our scientific literature.

THE BOTANICAL MANUALS AND THE IOWA FLORA

B. SHIMEK

The limited space in our ordinary botanical manuals does not permit a full discussion of variations in form, structure, habit, and geographic distribution. As a consequence imperfections and omissions appear which are often confusing and misleading to the user of the manual.

The two manuals, Gray's and Britton's, which are most frequently used for purposes of identification in Iowa, contain many inaccuracies of this character. Some of them are due to the limitations naturally placed on such works, but others are due to misunderstanding or error. The following notes on some of the more striking of these errors and omissions are offered, not in a spirit of criticism, but to help the students of our flora who are often misled by them.

No attempt is here made to discuss variations in taxonomic characters. Considering their necessarily brief descriptions the manuals cover these variations remarkably well, especially if both are consulted. These notes are limited to a discussion of habitat and geographic distribution.

The nomenclature of Gray's Manual, 7th ed., is employed in the main in this paper. Where the generic name differs in Britton's Manual it follows in parenthesis. As these notes are intended primarily for users of the manuals, common names and author's names are omitted, as they can be obtained from the manuals.

Where a note refers to but one of the manuals it is followed by the initial letter in parenthesis, (G.) for Gray and (B.) for Britton.

I HABITATS

It is impossible to give a full and accurate statement of habitats within the narrow limits of the manuals. It is

especially difficult to indicate the variations within the major habitats which we generally designate as swamps, forests, prairies, and sandy areas. The variations in the major habitats as displayed in Iowa are here indicated briefly under each head.

Swamp species. Comparatively few corrections need to be made for Iowa in this group.

Angelica atropurpurea is said to occur in alluvial soils (G.), but in Iowa it occurs in bogs.

Both manuals state that *Phlox maculata* is found in woods and along streams. In Iowa it occurs in boggy places, especially in the prairie sections.

Aster umbellatus is reported from moist thickets, but it occurs chiefly in prairie bogs, though sometimes entering the border thickets in swampy places.

Eleocharis Wolfii and *Solidago Riddellii* are said to occur on wet prairies, but the former usually grows in the shallow edges of ponds, and the latter in prairie bogs.

In a number of cases there are consistent differences between the floras of prairie and woodland bogs which are not brought out in the manuals. Thus both *Calla palustris* and *Symplocarpus foetidus* are referred to bogs, the latter also to wet soils (B.), but the former occurs (very rarely) in prairie bogs, while the latter grows in bogs (often of the "hanging" type), in wooded sections.

Several species which are normally swamp species, and are so listed, may appear on apparently dry prairie which was swampy earlier in the season, or on upland prairie after a series of moist seasons. In the former case it may be necessary to visit the locality earlier in the season to ascertain the origin of this flora. In the latter case but few individuals usually occur, and it behooves the observer to avoid hasty conclusions from the presence of individual specimens in any case. The swamp species which most frequently stray in this manner to the upland prairie are *Iris versicolor*, *Habenaria leucophaea*, *Cicuta maculata* and *Stachys palustris*. They might easily be mistaken for prairie plants under such circumstances by the inexperienced observer.

Forest species. The number of corrections for true forest plants is also small. A larger number of errors occurs where

certain prairie species are ascribed to "woods."

As a rule the manuals make no distinction between alluvial, upland, and open woods, though their floras are more or less distinct.

Notes on the following true woodland species are of interest.

Cypripedium hirsutum is recorded as occurring in swamps and woods, but in Iowa it is found in deep woods, usually on upland slopes.

Alnus rhamniifolia is reported in both manuals as a swamp plant. Its only known locality in Iowa is well up on a bluff where there is no evidence of swampy conditions.

Osmunda Claytoniana is reported from low grounds (G.) and moist places (B.). In Iowa it occurs chiefly on well-wooded upland slopes, especially near the heads of ravines.

Both manuals give the habitat "rich soil" for *Quercus macrocarpa* and *Actinomeris alternifolia*. The former frequently grows in poor, dry upland soils, and then becomes stunted, and the latter is found on rich wooded bottomlands.

Mitella diphylla and *Asarum canadense* var. *reflexum* and var. *acuminatum* are similarly credited to "rich woods." The *Mitella* usually grows on woody rocky slopes or ledges. The *Asarums* grow in rich woods, but var. *acuminatum* is usually found on slopes (often rocky), while var. *reflexum* is common in lower alluvial woods, only occasionally ascending to upland woods.

Smilax ecirrhata, reported in dry soil (G.), or without habitat (B.), is found in deeper woods, especially on upland slopes.

Gaylussacia baccata, credited to "woodlands and swamps" (G.) and to "woods and thickets" (B.), has been found only in dry upland woods.

Hamamelis virginiana is reported from "damp woods" (G.) and "low woods" (B.). In Iowa (northeastern part) this species is always found on wooded (often rocky) slopes.

Aster Drummondii is said to grow in "open ground" (G.), and in "dry soil, borders of woods and prairies" (B.). In Iowa it is common in upland woods. It seems to blend with *A. sagittifolius* which is frequent in more open places, and this may have caused confusion.

Phegopteris hexagonoptera occurs in rather deep, mostly up-

land woods, but is credited to "rather open woods" (G.), and "dry woods" (B.).

Certain other species frequently occur in woods but are properly credited to other habitats in which they also occur. *Eupatorium purpureum* is reported from "moist soil" (B.), but occurs both in swamps and in deep woods. *Erigeron annuus*, credited to "fields" (B.), and "fields and waste places" (G.) also frequently occurs on wooded banks and slopes.

Prairie plants. A number of species credited to woods in the manuals belong properly to the prairies and open places. Their occurrence in woods is exceptional, and they then appear as a rule in very open woods on ridges, or in the thin prairie groves which consist largely of smaller and more or less scattered bur oaks, etc. In such places the undergrowth is made up of prairie plants, forest plants being absent or exceptional, yet they would be reported as found "in woods." In addition to the few properly recorded from "prairies and open or dry woods," the following species, normally of the prairies and only exceptionally in thin open woods, should be noted: *Ranunculus fascicularis*, *Heuchera hispida*, *Oxalis violacea*, and *Silene stellata* reported (B.) from "woods," the last also from "wooded banks" (G.); *Scrophularia leporella* from "rich open woods" (G.) and "woods and along roadsides" (B.); *Amphicarpa (Falcata) Pitcheri* from "rich woods and thickets" (G.) and "moist thickets" (B.); *Zizia aurea* from "river-banks, meadows, and rich woods" (G.); *Ceanothus americanus* from "woodlands and gravelly shores" (G.) and "dry open woods" (B.); *Ancmone cylindrica* from "rocky woods and dry barrens" (G.) and "open places" (B.); *Polygala Senega* from "rocky woods" (B.) and "rocky soil" (G.); *Desmodium (Meibomia) canadense* from "open woods and banks of streams" (G.); *Lathyrus venosus* from "shady banks" (G.) and "river shores and banks" (B.); *Solidago serotina* from "thickets" (G.); *Pycnanthemum flexuosum* from "fields and thickets" (B.); *Fragaria virginiana* from "moist woodlands, fields, etc." (G.) and "dry soil" (B.); *Veronica (Leptandra) virginica* from "meadows, moist woods, thickets" (B.) and "rich soil" (G.); *Pedicularis canadensis* from "copses and woodlands" (B.) and "alluvial soil" (G.); *Hypoxis hirsuta* from "meadows and open woods" (G.) and "dry soil" (B.); and *Lilium philadelphicum* from "dry woods" (B.).

In addition to the foregoing prairie species reported from woods, a large number of other species, likewise of the prairies, have the habitat given indefinitely or erroneously. The most frequent indefinite designation of the habitat as "dry soil," "dry banks," "fields," "dry sand and gravel," etc., occurs with the following species which distinctly belong with the prairie flora in Iowa: *Andropogon scoparius*, *A. furcatus* (G.), *Sorghastrum nutans*, *Koeleria cristata*, *Bouteloua curtipendula*, *B. hirsuta*, *Hordeum jubatum* (B.), *Carex festucacea* (G.), *Carex straminea*, *C. pennsylvanica*, *Lilium philadelphicum* (G.), *Salix humilis*, *Comandra umbellata*, *Polygonum ramosissimum* (saline soil B.), *Chenopodium leptophyllum* (B.), *Oxybaphus nyctagineus* (B.), *O. floribundus* (B.), *O. hirsutus* (B.), *Lepidium apetalum*, *Potentilla arguta*, *P. canadensis*, *P. monspeliensis*, *Psoralea argophylla*, *P. esculenta*, *Astragalus canadensis* (G.), *Desmodium illinoense* (G.), *Lespedeza capitata*, *Vicia americana* var. *angustifolia* (B.), *Linum sulcatum*, *Polygala verticillata* (G.), *Euphorbia Preslii*, *E. corollata*, *Rhus glabra*, *Ceanothus ovatus* (G.), *Helianthemum canadense*, *Oenothera* (*Meriolix*) *serrulata*, *Gaura biennis*, *G. parviflorum* (B.), *Asclepias tuberosa*, *A. verticillata* (B.), *Acerates viridiflora* and varieties, *Phlox pilosa*, *Lithospermum canescens* (B.), *Ruellia ciliosa*, *Kuhnia eupatoroides* and var. *corymbulosa*, *Liatris* (*Lacinaria*) *cylindracea*, *L. punctata* (B.), *L. squarrosa*, *L. scariosa*, *Solidago speciosa* var. *angustata* (G.), *S. nemoralis*, *S. rigida*, *Aster laevis*, *A. multiflorus*, *A. ptarmicoides*, *Antennaria plantaginifolia*, *Parthenium integrifolium*, *Heliopsis scabra* (B.), *Rudbeckia hirta*, *Brauneria angustifolia* (G.), *B. pallida* (habitat omitted in Gray), *Lepachys* (*Ratibida*) *pinnata* (G.), *Helianthus grosseserratus* (often in rather moist places), *Achillea millefolium*, *Artemisia ludoviciana* (G.), *Cirsium* (*Carduus*) *discolor*, *C. Hillii*, *Lactuca ludoviciana* (B.), and *Lygodesmia juncea*.

The following prairie species are reported in the manuals as inhabiting rocky or sandy places: *Allium stellatum*, *Potentilla arguta*, *Acerates viridiflora* and its varieties, *Galium boreale*, and *Polygala Senega*. These species may occur on rocky hillsides, but they are commonly found on ordinary prairie.

The reported habitats of still other prairie plants are misleading. Thus, *Polygonum ramosissimum* is said to be found in saline soils (B.); *Astragalus canadensis* along streams (B.); *Lathyrus venosus* from river-banks (B.); *Convolvulus sepium* in alluvial soils or along streams (G.); and *Smilacina stellata* from

moist banks (G.) and moist soil (B.); yet all these species occur freely upon the prairie.

Species of sandy areas. The majority of our prairie plants may be found also upon sandy areas. Certain species, however, are quite characteristic of sand and gravel habitats, but in some cases the record of their habitat is quite misleading.

Thus, *Cyperus filiculmis* is reported from dry soil (G.) and dry fields and hills (B.); *Polygonum tenue* from dry soil; *Froelichia floridana* from dry soil (B.); *Polanisia trachysperma* from prairies (B.); *Cristatella Jamesii* from dry soil (B.); *Potentilla paradoxa* from prairies and river-banks (G.) and shores and river-banks (B.); *Ptelea trifoliata* from rocky places (G.) and prairies (B.); *Rhus canadensis* from dry rocky banks; *Viola pedata* from dry fields and hillsides (B.); *Androsace occidentalis* from bare hills and barrens (G.) and dry soil (B.); *Lithospermum Gmelini* from dry woods (B.); *Synthyris Bullii* from oak barrens and prairies (G.) and dry prairies (B.); *Houstonia minima* from dry hills (G.) and dry soil (B.); *Aster linariifolius* from dry soil (G.) and dry or rocky soil (B.); *Ambrosia psilostachya* from prairies and plains (G.) and moist open soil (B.); *Helianthus petiolaris* from dry prairies (B.); and *Helianthus occidentalis* from dry barrens (G.) and dry soil (B.).

In Iowa all these species occur on sand, or on very sandy soil.

In quite a number of cases both manuals fail to record the habitat.

Contradictory references to habitat are made in a number of places. Thus the habitat of *Urtica gracilis* is given as moist ground (G.) and dry soil (B.); of *Apocynum cannabinum* as gravelly and sandy soil (G.) and fields and thickets (B.); of *Polygonum ramosissimum* as dry sandy soil (G.) and saline soil (B.); of *Ranunculus fascicularis* as dry or moist hills (G.) and woods (B.); of *Lilium philadelphicum* as dry or sandy ground (G.) and dry woods (B.); of *Physalis pruinosa* as sandy soil (G.) and cultivated soil (B.); of *Physalis virginiana* as dry hills, gravelly soils, etc. (G.) and rich soil (B.); of *Hypoxis hirsuta* as meadows and open woods (G.) and dry soil (B.); and of *Castilleja coccinea* as low sandy ground (G.) and meadows and thickets (B.). Most of these species belong in the main to the prairie flora, the first in rather low ground.

The chief causes of the inaccurate habitat references seem to lie in the failure of the manuals to recognize the prairie properly, and in a lack of differentiation of our forested areas. The mere reference to "woods" is very unsatisfactory, for we have alluvial woods, the woods of lower slopes, and upland woods, besides the prairie groves and thickets, and each presents floral peculiarities which are worthy of note.

II. GEOGRAPHIC DISTRIBUTION

Geographic distribution is particularly difficult to indicate accurately in the limited space of the manuals. Most plants are irregularly distributed, and not a few are very local and the localities are often widely separated. Within the limits, as indicated, many species may be lacking entirely over areas of considerable extent, while they are common in other parts.

The manuals have scarcely done justice, however, to the Iowa flora, a fact difficult to explain since numerous papers, published by working botanists, have set out its composition quite fully. These papers are evidently either unknown to the eastern authors of the manuals, or have been ignored by them.

The distribution of a large number of species, as given in the manuals, is such that Iowa would scarcely be included. In quite a number of cases there is doubt because the limits of distribution are rather indefinite, but the following species would probably be considered by the less-experienced worker as excluded from our flora by both manuals, though all are found in Iowa:

<i>Digitaria</i> (Syntherisma) filiformis	<i>Vaccinium vacillans</i> (close in Britton)
<i>Quercus palustris</i> (less clearly in Britton)	<i>Primula mistassinica</i>
<i>Quercus lyrata</i>	<i>Gilia</i> (<i>Collomia</i>) <i>linearis</i> (close in Gray)
<i>Ranunculus Purshii</i>	<i>Physostegia parviflora</i>
<i>Clematis verticillata</i> (<i>Atragene americana</i>)	<i>Chelone obliqua</i>
<i>Cardamine Douglassii</i> (purea)	<i>Houstonia angustifolia</i>
<i>Potentilla</i> (<i>Sibbaldiopsis</i>) <i>tridentata</i>	<i>Diervilla Lonicera</i> (<i>Diervilla</i>)
	<i>Lonicera canadensis</i>
	<i>Linnaea borealis</i> v. <i>americana</i>
	<i>Viburnum dentatum</i>

<i>Prunus pumila</i>	<i>Solidago tenuifolia</i> (<i>Euthamia</i>
<i>Acalypha gracilens</i>	<i>caroliniana</i>)
<i>Lechea minor</i>	<i>Lygodesmia rostrata</i>
<i>Vaccinium pennsylvanicum</i>	

Of these species *Clematis verticillata*, *Potentilla tridentata*, *Vaccinium pennsylvanicum*, *V. vacillans*, *Linnaea borealis* var., *Solidago tenuifolia* and *Diervilla Lonicera*, seem to be confined to north-eastern Iowa, where they are local in distribution; *Prunus pumila* occurs rarely in the extreme northeastern and north-western parts; *Chelone obliqua*, local north and east; *Ranunculus Purshii* and *Gilia linearis* in the northwestern part; *Houstonia angustifolia* and *Lygodesmia rostrata* in the western part; *Primula mistassinica* rarely in the central part; and *Quercus palustris* and *Q. lyrata* in the southeastern part, the latter being rare.

The following species are similarly excluded by Gray's Manual:

<i>Woodsia ilvensis</i>	<i>Calla palustris</i>
<i>Paspalum ciliatifolium</i>	<i>Zygadenus chloranthus</i> (near)
<i>Panicum latifolium</i>	<i>Habenaria Hookeri</i> (near)
<i>Sphenopholis</i> (<i>Eatonia</i>) <i>obtusata</i>	<i>Astragalus plattensis</i>
<i>Hordeum pusillum</i>	<i>Viola lanceolata</i>

Of these species *Woodsia ilvensis* and *Habenaria Hookeri* are rare in the northeastern part of the state; *Calla palustris* is rare in the north-central part; *Astragalus plattensis* is found in the far western part; *Viola lanceolata* in the Cedar River Valley at two widely separated points; and the remaining species are more widely distributed, especially in the northern and eastern parts of the state.

The following species in Britton's Manual do not have their range include Iowa:

<i>Woodsia scopulina</i>	<i>Melica Porteri</i> (<i>parviflora</i>)
<i>Asplenium angustifolium</i>	<i>Betula lutea</i>
<i>Cystopteris</i> (<i>Filix</i>) <i>bulbifera</i>	<i>Quercus bicolor</i> (<i>platanoides</i>)
<i>Equisetum sylvaticum</i>	<i>Coptis trifolia</i>
<i>Lycopodium complanatum</i>	<i>Jeffersonia diphylla</i>
<i>Lycopodium clavatum</i>	<i>Cristatella Jamesii</i>
<i>Abies balsamea</i>	<i>Physocarpus</i> (<i>Opulaster</i>)
<i>Potamogeton praelongus</i>	<i>opulifolius</i>

<i>Agrimonia striata</i>	<i>Tecoma radicans</i>
<i>Rosa blanda</i>	<i>Houstonia minima</i>
<i>Amelanchier spicata</i>	<i>Lonicera Sullivantii</i>
<i>Oxytropis (Aragallus) Lamberti</i>	<i>Kuhnia eupatoroides</i>
<i>Croton monanthogynus</i>	<i>Rudbeckia subtomentosa</i>
<i>Acer spicatum</i>	<i>Brauneria purpurea</i>
<i>Steironema quadrifolium</i>	<i>Coreopsis tripteris</i>
<i>Phlox bifida</i>	<i>Bidens aristosa</i>
<i>Lippia lanceolata</i>	<i>Artemisia frigida</i>
<i>Lycopus rubellus</i>	<i>Hieracium canadense</i>

Of this series *Woodsia scopulina* and *Artemisia frigida* are found in the extreme northwestern part of the state, while *Oxytropis Lamberti* is more widely distributed in the west and northwest; *Amelanchier spicata*, *Steironema quadrifolium* and *Potamogeton praelongus* in the northern part; *Asplenium angustifolium*, *Abies balsamea*, *Coptis trifolia*, *Jeffersonia diphylla*, *Betula lutea* and *Acer spicatum* are local and limited to the northeastern part, the *Betula* also occurring in the north-central part; *Lycopodium clavatum*, *L. complanatum*, and *Phlox bifida* are local in the eastern part, while *Cystopteris bulbifera*, *Equisetum sylvaticum* and *Quercus bicolor* are more widely distributed in the same section; *Melica Porteri*, *Tecoma radicans*, *Croton monanthogynus*, *Houstonia minima*, and *Brauneria purpurea* are southeasterly in distribution; while the remaining species are more widely distributed, chiefly over the eastern half of the state.

In a few cases it is evident that species are erroneously credited to Iowa in the manuals, not always through any fault of their authors. Thus, one of the reports of *Isoetes melanopoda* is based on the phyllodial state of *Sagittaria heterophylla* according to Cratty, who examined the material at Ames on which the report was founded, and the writer was unable to find verification of earlier records.

The report of *Betula lenta* is based on *B. lutea* which was at first erroneously identified as *B. lenta*. A few trees in Clayton County, northeastern Iowa, are, however, probably *B. lenta*. A more critical study of this material is being made, and *B. lenta* may be restored to the Iowa list.

Robinia pseudoacacia (B.), *Diospyros virginiana*, and *Sassafras*

variifolium (G.) are credited to Iowa, but the writer has been unable to verify the occurrence of native plants. The Robinia was introduced early for ornamental purposes, and has become widely distributed in eastern Iowa, but no authentic native specimens have been encountered. Diospyros and Sassafras are planted in southern Iowa, and both may occasionally escape from cultivation. Both species were probably introduced by southern people into that part of the state in its early history,—the one for its fruit and the other for its reputed medicinal properties.

The writer has been unable to find any authentic evidence which would show that *Polypodium polypodioides* (G.), *Cladium mariscoides* (G.), *Sarracenia purpurea* (G.), and *Silphium terebinthinaceum* (B.) are native to Iowa. The last species should be found in eastern Iowa as it is not rare in adjacent parts of Illinois, but no authentic case of its occurrence has been found by the writer. If present, it is exceedingly limited in distribution.

A small number of species native to the state is omitted entirely from the manuals. Thus, Gray omits *Cristatella Jamesii*, and Britton omits *Cirsium canescens* and *C. iowensis*. In several other cases certain named forms are omitted because of doubt as to the validity of the species. This is true, for example, in the genera *Aster*, *Xanthium*, *Rudbeckia*, and *Helianthus*, in which Britton recognizes a larger number of forms as distinct species. Some of the more striking cases of this kind are given in the comparative list of Gray and Britton names in the closing part of this paper.

In other cases it will be found that the use of synonyms results in apparent omission of species. These also are given in the above-mentioned list.

Quite frequently students of the Iowa flora have complained that they could not find certain species which are credited to the state. In a number of cases this is due to the assignment of the species in the manual to the wrong part of the state. All of these sectional references are in Gray's Manual, those in Britton's Manual being general references to "Iowa." It is interesting to note that Gray refers 225 species and varieties to Iowa, while Britton makes 166 such references.

The species which are referred to the wrong section of the state in Gray are the following:

Pinus Strobus, reported from eastern Iowa, but found also in the north-central part.

Abies balsamea, to central Iowa, but the species is limited to the northeast corner of the state.

Carex stenophylla, from northern Iowa, but found only in the northwestern part.

Erythronium mesochoreum, from western Iowa, but occurring across the two southern tiers of counties.

Betula alba var. *papyrifera*, from northern Iowa, but properly chiefly from the northeastern part, though a few occur in the north-central portion.

Alnus incana, from northern Iowa, but limited to the northeastern part.

Asimina triloba, from northeastern Iowa. This should read "southeastern."

Rubus triflorus, from northern Iowa, should be limited to northeastern Iowa.

Acer spicatum, from eastern Iowa, also limited to the northeastern part.

Mentzelia decapetala, from the western part, should be "northwestern."

Panax quinquefolia, from eastern Iowa. This species was formerly abundant at least as far west as Winnebago County in the north-central part.

Lonicera Sullivantii, from "central Iowa," but it occurs throughout most of the eastern part of the state.

In quite a number of cases species which are more or less restricted in distribution are simply credited to "Iowa" in the manuals.

Both manuals refer the following species to "Iowa," but they are here grouped according to their more restricted distribution:

The northeastern quarter of the state:

Cryptogramma Stelleri

Phegopteris Robertiana

Taxus canadensis

Symplocarpus (Spathyema) foetidus

Lycopodium lucidulum

Northern Iowa:

Salix candida

Northwestern Iowa:

Beckmannia erucaeformis

Carex sychnocephala

Carex stenophylla

Southeastern Iowa:

Carya illinoensis (Hicoria Pecan)

Carya (Hicoria) *laciniosa*

Astragalus distortus

Synthyris Bullii (also local northward)

Gray's Manual similarly refers the following species to "Iowa," but they, too, are restricted as indicated:

Northeastern quarter of state:

Lycopodium complanatum var. *flabelliforme* (local and rare)

Salix rostrata (local)

Betula alba var. *cordifolia*

Chrysosplenium americanum

Sambucus racemosa (*S. pubens*)

Valeriana edulis

Northern Iowa:

Astragalus (*Phaca*) *neglectus*

Menyanthes trifoliata

Northwestern Iowa:

Marsilea vestita (very rare)

Opuntia fragilis (rare and local)

Senecio palustris (rare)

Western Iowa:

Aplopappus (*Sideranthus*) *spinulosus*

Central Iowa:

Stipa comata

Southern Iowa:

Quercus stellata

Southeastern Iowa:

Tecoma radicans

Brauneria purpurea

Phlox bifida (also local northward)

Eastern Iowa:

Phegopteris polypodioides (P. *Phegopteris*)

Aspidium (*Dryopteris*) *Goldianum*

Trillium nivale, chiefly eastward, but also westward to Sac and Cherokee Counties.

Schrankia uncinata is also reported from Iowa, but the writer has no authentic record of its occurrence in the state.

Britton's Manual likewise refers the following species to "Iowa," but they are found only in the sections indicated:

Northeastern Iowa:

Habenaria (*Lysias*) *Hookeri*

Adoxa Moschatellina (local)

Northern Iowa:

Calla palustris (very rare)

Salix pedicellaris

Northern and eastern Iowa:

Parnassia caroliniana (local)

Northwestern Iowa:

Amorpha microphylla (*nana*) (becoming rare)

Western half of Iowa:

Glycyrrhiza lepidota

Southern Iowa:

Erythronium mesochoreum (two southern tiers of counties)

Rhamnus lanceolata (southern half of state)

AEsculus octandra (south-central part)

Southeastern Iowa:

Carex laxiflora latifolia (*albursina*)

Commelina virginica

Eastern Iowa:

Betula nigra

Fraxinus quadrangulata

Viola pubescens is also more common eastward, though it extends across the state. Westward it is replaced largely by *V. scabriuscula*.

An additional reason for the difficulty with which some species are now found is their disappearance from large areas as a result of settlement and cultivation. This is true of many of our prairie, forest, and swamp species, which have been more and more restricted as their natural habitats were

destroyed. Notable examples among prairie plants are *Liatris* (*Lacinaria*) *squarrosa*, *Anemone caroliniana*, and *Amorpha microphylla* (*nana*); among forest plants the species of *Phegopteris* among ferns, the forest species of *Cypripedium*, and the brilliant *Lobelia cardinalis* of bottomland woods; and among swamp plants *Pontederia cordata*, *Calopogon pulchellus*, and *Gentiana crinita*.

Additional trouble is caused by the omission of the geographic distribution in several cases.

SYNONYMS

Most of the Iowa botanists have followed Gray's Manual, but several papers have appeared in which the nomenclature of Britton's Manual has been employed. To assist in clearing up the confusion caused by the use of the two systems, the following comparative list of the two sets of synonyms is presented as far as it applies to the Iowa flora.

Where the difference is in generic names and the specific names are not changed, only the former are given.

The common names and authors' names are again omitted, as they may be obtained from the manuals.

For convenience in reference the names from Britton's Manual are arranged alphabetically in the first column and the corresponding Gray synonyms are given in the second column, just opposite. This is necessary as Britton omits most of the Gray synonyms, while Gray's Manual gives the Britton synonyms quite fully.

List of Iowa Synonyms

Britton	Gray
Abutilon Abutilon	A. Theophrasti
Acerates viridiflora Ivesii	A. viridiflora lanceolata
Acroanthus	Microstylis
Acuan	Desmanthus
Adicea	Pilea
Adopogon	Krigia
Agastache anethiodora	A. Foeniculum
Agrimonia Brittoniana	A. striata
Agrimonia hirsuta	A. gryposepala
Agropyron spicatum	A. Smithii
Allionia	Oxybaphus

Allionia lanceolata	Oxybaphus albidus
Alsine	Stellaria
Amelanchier Botryapium	A. oblongifolia
Amorpha nana	A. microphylla
Ampelopsis cordata	Cissus Ampelopsis
Amygdalus persica	Prunus
Apios Apios	A. tuberosa
Arabis brachycarpa	A. Drummondii
Aragallus	Oxytropis
Aristida longiseta	A. purpurea
Aronia nigra	Pyrus melanocarpa
Asclepias exaltata	A. phytolaccoides
Astragalus carolinianus	A. canadensis
Astragalus crassicaupus	A. caryocarpus
Atheropogon curtipendula	Bouteloua
Atragene americana	Clematis verticillata
Batrachium divaricatum	Ranunculus circinatus
Batrachium trichophyllum	Ranunculus aquatilis
	capillaceus
Blephariglottis leucophaea	Habenaria
Boebera	Dyssodia
Bradleya	Wisteria
Brasenia purpurea	B. Schreberi
Bulbilis	Buchloe
Bursa	Capsella
Butneria	Calycanthus
Capnoides	Corydalis
Cardamine purpurea	C. Douglassii
Carduus	Cirsium
Carex albursina	C. laxiflora latifolia
Carex cristatella	C. cristata
Carex Haydeni	C. stricta decora
Carex interior	C. scirpoides
Carex pedicellata	C. communis
Carex setifolia	C. eburnea
Carex sterilis	C. stellulata
Carex teretiuscula	C. diandra
Carex teretiuscula prairie	C. diandra ramosa
Carex tribuloides moniliforme	C. tribuloides reducta
Carex xanthocarpa	C. setacea

<i>Cassia marilandica</i>	<i>C. Metzgeri</i> (in part)
<i>Catalpa Catalpa</i>	<i>C. bignonioides</i>
<i>Cerastium longipedunculata</i>	<i>C. nutans</i>
<i>Chaetochloa</i>	<i>Setaria</i>
<i>Chamaenerion angustifolium</i>	<i>Epilobium</i>
<i>Chrysosplenium iowensis</i>	<i>C. tetrandrum</i>
<i>Citrullus Citrullus</i>	<i>C. vulgaris</i>
<i>Clematis missouriensis</i>	<i>C. virginiana</i> (in part)
<i>Clematis Simsii</i>	<i>C. Pitcheri</i>
<i>Collomia</i>	<i>Gilia</i>
<i>Comarum palustris</i>	<i>Potentilla</i>
<i>Corallorhiza multiflora</i>	<i>C. maculata</i>
<i>Cracca</i>	<i>Tephrosia</i>
<i>Crataegus Brownii</i>	<i>C. Margaretta</i>
<i>Crataegus campestris</i>	<i>C. pertomentosa</i>
<i>Crataegus Eggerti</i>	<i>C. coccinoides</i>
<i>Crataegus uniflora</i>	<i>C. tomentosa</i>
<i>Cuscuta paradoxa</i>	<i>C. glomerata</i>
<i>Cynoglossum virginicum</i>	<i>C. virginiana</i> and <i>C. boreale</i>
<i>Cyperus inflexus</i>	<i>C. aristatus</i>
<i>Cyperus speciosus</i>	<i>C. ferax</i>
<i>Cypripedium hirsutum</i>	<i>C. parviflorum</i>
<i>Cypripedium reginae</i>	<i>C. hirsutum</i>
<i>Dasyphora fruticosa</i>	<i>Potentilla</i>
<i>Dasystoma</i>	<i>Gerardia</i>
<i>Dasystoma Besseyana</i>	<i>Gerardia tenuifolia</i>
	<i>macrophylla</i>
<i>Dasystoma Gattingeri</i>	<i>Gerardia tenuifolia</i>
<i>Delphinium albescens</i>	<i>D. Penardi</i>
<i>Deringa</i>	<i>Cryptotaenia</i>
<i>Diervilla Diervilla</i>	<i>D. Lonicera</i>
<i>Diplachne</i>	<i>Leptochloa</i>
<i>Doellingeria umbellata</i>	<i>Aster</i>
<i>Drymocallis arguta</i>	<i>Potentilla</i>
<i>Eatonia</i>	<i>Sphenopholis</i>
<i>Eatonia pennsylvanica</i>	<i>Sphenopholis pallens</i>
<i>Eragrostis Eragrostis</i>	<i>E. minor</i>
<i>Eragrostis major</i>	<i>E. megastachya</i>
<i>Eriophorum polystachyon</i>	<i>E. angustifolium</i>

<i>Eryngium aquaticum</i>	<i>E. yuccifolium</i>
<i>Eupatorium ageratoides</i>	<i>E. urticaefolium</i>
<i>Euphorbia arkansana</i>	<i>E. dictyosperma</i> (in part)
<i>Euphorbia missouriensis</i>	<i>E. dictyosperma</i> (in part)
<i>Euphorbia nutans</i>	<i>E. Preslii</i>
<i>Euthamia caroliniana</i>	<i>Solidago tenuifolia</i>
<i>Euthamia graminifolia</i>	<i>Solidago</i>
<i>Falcata</i>	<i>Amphicarpa</i>
<i>Froelichia campestris</i>	<i>F. floridana</i>
<i>Galeorchis</i>	<i>Orchis</i>
<i>Gaylussacia resinosa</i>	<i>G. baccata</i>
<i>Glecoma</i>	<i>Nepeta</i>
<i>Gnaphalium obtusifolium</i>	<i>G. polycephalum</i>
<i>Gymnadeniopsis clavellata</i>	<i>Habenaria</i>
<i>Gyrostachys</i>	<i>Spiranthes</i>
<i>Hepatica acuta</i>	<i>H. acutiloba</i>
<i>Hepatica Hepatica</i>	<i>H. triloba</i>
<i>Hicoria minima</i>	<i>Carya cordiformis</i>
<i>Hicoria Pecan</i>	<i>Carya illinoensis</i>
<i>Homalocenchrus virginicus</i>	<i>Leersia</i>
<i>Hypericum maculatum</i>	<i>H. punctatum</i>
<i>Hypericum Sarothra</i>	<i>H. gentianoides</i>
<i>Hypericum sphaerocarpum</i>	<i>H. cistifolium</i>
<i>Hypopitys americana</i>	<i>Monotropa Hypopitys</i> (in part)
<i>Hypopitys lanuginosa</i>	<i>Monotropa Hypopitys</i> (in part)
<i>Hystrix Hystrix</i>	<i>H. patula</i>
<i>Impatiens aurea</i>	<i>I. pallida</i>
<i>Ionactis linariifolius</i>	<i>Aster</i>
<i>Juncoides pilosum</i>	<i>Luzula saltensis</i>
<i>Juncus acuminatus</i>	<i>J. debilis</i>
<i>Juniperus Sabina</i>	<i>J. horizontalis</i>
<i>Kneiffia fruticosa</i>	<i>Oenothera</i>
<i>Koellia</i>	<i>Pycnanthemum</i>
<i>Kuhnia glutinosa</i>	<i>K. eupatoroides corymbulosa</i>
<i>Kuhnistera</i>	<i>Petalostemum</i>
<i>Lacinaria</i>	<i>Liatris</i>
<i>Lactuca virosa</i>	<i>L. scariola integrata</i>
<i>Lappula Lappula</i>	<i>L. echinata</i>
<i>Lappula texana</i>	<i>L. Redowskii occidentalis</i>

Lepargyrea	Shepherdia
Leptandra virginica	Veronica
Leptilon canadensis	Erigeron
Leptilon divaricatus	Erigeron
Leptorchis	Liparis
Lilium umbellatum	L. philadelphicum andinum
Limnorchis hyperborea	Habenaria
Limodorum tuberosum	Calopogon pulchellus
Linaria Linaria	L. vulgaris
Lithospermum linearifolium	L. angustifolium
Lolium italicum	L. multiflorum
Lotus	Hosackia
Lycium vulgare	L. halimifolium
Lycopersicum Lycopersicum	L. esculentum
Lysias Hookeriana	Habenaria Hookeri
Lysias orbiculata	Habenaria
Macrocalyx	Ellisia
Malus ioensis	Pyrus
Malus Malus	Pyrus
Malus Souldardi	Pyrus
Matteucia Struthiopteris	Onoclea
Meibomia	Desmodium
Melica diffusa	M. nitens
Melica parviflora	M. Porteri
Meriolix serrulata	OEnothera
Mesadenia reniformis	Cacalia
Micrampelis	Echinocystis
Moeringia lateriflora	Arenaria
Monarda mollis	M. mollis (in part)
Monarda scabra	M. mollis (in part)
Monniera	Bacopa
Morongia	Schrankia
Muhlenbergia diffusa	M. Schreberi
Nabalus	Prenanthes
Naumburgia	Lysimachia
Nothocalais	Agoseris
Onagra biennis	OEnothera
Onagra strigosa	OEnothera muricata
Onosmodium molle	O. occidentalis (in part)
Opulaster	Physocarpus

<i>Opuntia humifusa</i>	<i>O. Rafinesquei</i>
<i>Oryzopsis melanocarpa</i>	<i>O. racemosa</i>
<i>Osmunda spectabilis</i>	<i>O. regalis</i>
<i>Oxalis Bushii</i>	<i>O. corniculata</i> (in part)
<i>Oxalis corniculata</i>	<i>O. corniculata</i> (in part)
<i>Oxalis cymosa</i>	<i>O. corniculata</i> (in part)
<i>Oxalis rufa</i>	<i>O. corniculata</i> (in part)
<i>Oxygraphis Cymbalaria</i>	<i>Ranunculus</i>
<i>Panicularia</i>	<i>Glyceria</i>
<i>Panicularia americana</i>	<i>Glyceria grandis</i>
<i>Panicularia brachyphylla</i>	<i>Glyceria fluitans</i>
<i>Panicum cognatum</i>	<i>Leptoloma</i>
<i>Panicum macrocarpon</i>	<i>P. latifolium</i>
<i>Panicum proliferum</i>	<i>P. dichotomiflorum</i>
<i>Parosela</i>	<i>Dalea</i>
<i>Parthenocissus</i>	<i>Psedera</i>
<i>Peramium</i>	<i>Epipactis</i>
<i>Phegopteris, Phegopteris</i>	<i>P. polypodioides</i>
<i>Philotria</i>	<i>Elodea</i>
<i>Phragmites Phragmites</i>	<i>P. communis</i>
<i>Poa flava</i>	<i>P. triflora</i>
<i>Polycodium stamineum</i>	<i>Vaccinium</i>
<i>Polygala virescens</i>	<i>P. sanguinea</i>
<i>Polygonum camporum</i>	<i>P. ramosissimum</i>
<i>Polygonum emersum</i>	<i>P. Muhlenbergii</i>
<i>Polygonum robustior</i>	<i>P. acre</i>
<i>Polygonum incarnatum</i>	<i>P. lapathifolium</i>
<i>Potamogeton lonchitis</i>	<i>P. americanus</i>
<i>Potamogeton Nuttallii</i>	<i>P. epihydrus</i>
<i>Pteridium</i>	<i>Pteris</i>
<i>Pulsatilla hirsutissima</i>	<i>Anemone patens Wolfgangiana</i>
<i>Pyrola rotundifolia</i>	<i>P. americana</i>
<i>Quamassia hyacinthina</i>	<i>Camassia esculenta</i>
<i>Quamoclit Quamoclit</i>	<i>Ipomoea</i>
<i>Quercus acuminata</i>	<i>Q. Muhlenbergii</i>
<i>Quercus minor</i>	<i>Q. stellata</i>
<i>Quercus platanoides</i>	<i>Q. bicolor</i>
<i>Quercus Schneckii</i>	<i>Q. texana</i>
<i>Ranunculus ovalis</i>	<i>R. rhomboideus</i>

Ratibida	Lepachys
Rhus aromatica	R. canadensis
Rhus Cotinus	R. cotinoides
Rhus hirta	R. typhina
Ribes rubrum	R. vulgare
Roripa	Radicula
Rosa arkansana	R. pratincola
Rosa lucida	R. virginiana
Rubus procumbens	R. villosus
Rubus strigosus	R. idaeus aculeatissimus
Rumex salicifolius	R. pallidus (in part)
Rumex salicifolius	R. mexicanus (in part)
Sagittaria cristata	S. graminea
Sagittaria rigida	S. heterophylla
Salix Bebbiana	S. rostrata
Salix interior	S. longifolia
Salmonia	Polygonatum
Sambucus pubens	S. racemosus
Sassafras Sassafras	S. variifolium
Savastana	Hierochloe
Scutellaria cordifolia	S. versicolor
Scutellaria incana	S. canescens
Sibbaldiopsis tridentata	Potentilla
Sideranthus	Aplopappus
Sieversia ciliata	Geum triflorum
Silene alba	S. nivea
Sinapsis	Brassica
Solidago flexicaulis	S. latifolia
Solidago rigidiuscula	S. speciosa angustata
Sophia pinnata	Sisymbrium canescens
Sorbus Aucuparia	Pyrus
Sorghastrum avenaceum	S. nutans
Spartina cynosuroides	S. Michauxiana
Spathyema	Symplocarpus
Sporobolus cuspidatus	S. brevifolius
Sporobolus longifolius	S. asper
Stenophragma Thaliana	Sisymbrium
Symphoricarpos	
Symphoricarpos	S. orbiculatus

Syndesmon	Anemonella
Synosma suaveolens	Cacalia
Syntherisma	Digitaria
Taraxacum Taraxacum	T. officinale
Thalesia	Orobanche
Thalictrum purpurascens	T. dasycarpum
Thaspium trifoliatum	T. aureum atropurpureum
Tricuspid seslerioides	Tridens flavus
Trifolium aureum	T. agrarium
Triphora	Pogonia
Unifolium	Maianthemum
Uvularia sessilifolia	Oakesia
Vaccaria	Saponaria
Vagnera	Smilacina
Verbesina	Actinomeris
Vicia linearis	V. angustifolia
Washingtonia	Osmorrhiza
Zygadenus elegans	Z. chloranthus

ECOLOGICAL CONDITIONS DURING LOESS-DEPOSITION

B. SHIMEK

The climatic and other physical conditions under which the deposition of our American loess has taken place have invited both study and speculation ever since scientific observers entered the Mississippi Valley. The result has been a varied assortment of hypotheses and conclusions relative to the agencies which have been concerned in the work of deposition, duplicating in fact the diversity of views concerning the origin of the loess of Europe and China.

For more than half a century after the publication of Cornelius' paper in 1818 (22)¹ there was practical unanimity in the acceptance of the subaqueous mode of deposition as most plausible. Many modifications of the fundamental concept that the loess was formed in water were, however, presented by various writers.

Cornelius himself regarded the "clays" (now known as loess) of Natchez, Mississippi, as alluvial, and this view was widely accepted by a distinguished line of geologists until comparatively recent time, swollen streams being regarded as the agency of transportation and deposition by most writers (7, 16, 18, 21, 24, 42).

Some, however, have regarded the deposit as lacustrine, dammed rivers or thawed basins in glacial ice forming the necessary lakes (6, 19, 20, 23, 26, 34, 38, 41, 43, 65, 68, 69, 70, 71, 74); still others connected it with outwash from the retreating front of the glaciers (5, 12, 13, 35, 36, 44, 47, 72); and a few even regarded it as marine (30, 33).

When Richthofen in 1870 (45) presented his first suggestion of eolian origin for the great loess deposits of China, and followed it with a series of papers in which he set out his views

¹The numbers in parentheses throughout this paper refer to the bibliography.

more fully (especially in 46), there was developed a general disposition not to accept this explanation for the American loess, however plausible it might appear in China where adjacent deserts could furnish enormous amounts of dust.

Richthofen based his conclusion that loess was of eolian and not aqueous origin chiefly on the varying altitudes at which it occurs, on the absence of stratification, on the fauna consisting of land shells, and on the presence of root-marks.

The most vigorous objection to this view was expressed by Todd in a paper (widely approved at the time by American geologists) published in 1879 (66), in which he attempted to show that the inequalities in altitude in our loess could be accounted for by assuming its deposition in the huge Lake Missouri, presumably covering all our loess area; that there is lamination if not stratification in the loess; that there are "semi-aquatic" and aquatic shells in the loess; that root-marks in the loess are formed by deep-rooted modern plants; and that the loess resembles the present deposits of the Missouri, while its deposition would require a great elevation on the seaward side to keep out moisture.

Curiously, every one of these arguments fails. If a great lake covered the loess region there were no immediate land-surfaces on which the land shells could develop; there is lamination in the loess, but it follows surface contours after the dune fashion; the shells called "semi-aquatic" by Todd are strictly terrestrial, and the one aquatic pulmonate, *Lamnaea humilis*, which he mentions, is very local and not common in the loess; there are buried root-marks as is shown in many sections in the Upper Mississippi Valley (for examples see 60, pl. VII, fig. 1); only some of the present deposits of the Missouri resemble loess, and they have been washed down from the bordering loess bluffs; and there is no need of presuming that desert areas had to be created by great elevations to account for the source of loess dust.

The greatest obstacle to the aqueous concept of loess-deposition is presented by the wide prevalence within it of the shells of terrestrial mollusks. The force of this obstacle was weakened in the minds of many by misstatements with which references to these fossils fairly bristle, and which must have

resulted from a lack of first-hand knowledge of the habits and character of this fauna.

Thus, Humphreys and Abbot (31) speak of "vast numbers of freshwater shells," Foster (26) states that the shells are all freshwater; Bannister (3, 4) and Green (28, 29) speak only of freshwater shells; while a large number of earlier (and some more recent) writers place the emphasis on the aquatic species by referring to "freshwater and land shells" (8, 37, 74), or, in one case (37), to "lacustrine, fluviatile, amphibious and land shells."

In some cases the habits of the fossil species have been given incorrectly. Thus *Helicina occulta* and *Pomatiopsis lapidaria* (9, 10, 11, also 52, 56, 57) have been repeatedly listed as aquatic (though both are truly terrestrial) simply because they have the operculum of our aquatic prosobranchs. The species of Succinea are frequently listed as "amphibious" or "semi-aquatic" (24, 38). This designation might apply only to one species, namely, *S. retusa*, and that is exceedingly rare in loess. The species which predominate in the loess, namely, *S. ovalis*, *S. avara*, and *S. grosvenori*, are strictly terrestrial, the last especially occurring in dry, often high places.

In many cases the references to the abundance of the few aquatic pulmonates which have been found in the loess have been careless or exaggerated. Thus, Todd (66) states that *Limnaea humilis* is "quite abundant" in the western loess. The experience of the writer, covering more than 50 years in the field, has shown that all the forms which have been included under that name are very local, quite rare, and not scattered through the loess, but restricted to belts or pockets which represent the bottoms or edges of buried shallow ponds (50, 51, 52). Baker (2) reports a related species, *Lymnaea* (*Fossaria*) *parva* as "common" in a loess exposure in the S.W. $\frac{1}{4}$, S.W. $\frac{1}{4}$, Sec. 14, T. 5 N., R. 4 E. As a matter of fact, the shells of *Lymnaea* in this exposure are practically, if not wholly, restricted to narrow belts or lenses of material which is not loess, and which probably represents successive edges of a pond, or the border of a sluggish stream. In 1880 Call (8), in a paper in which he states that the "lacustrine origin (of the loess) is now a quite generally conceded point," re-

ports Physa, Limnophysa, Planorbis, and perhaps Ancylus, as "found throughout the loess mingled with land shells—." Physa and Planorbis are exceedingly rare in the loess, and Ancylus is scarcely known, while Limnophysa (*Lymnaea*, etc.) is very local and restricted as noted above. All these genera include freshwater pulmonates which usually live in shallow ponds, and if more than a rarely occasional shell is present, they are found in belts or pockets suggesting the bottom or edges of shallow ponds or sluggish streams (50, 51, 52). Other specific cases might be cited, but these will serve to illustrate the point.

Another misleading factor has been the frequent reporting of fossils from the loess when in reality they belonged to some other formation, geological or human.

Most if not all of the vertebrate "loess" fossils of the Mississippi Valley are of this type; Aftonian fossil shells have been so reported; alluvial and lacustral deposits have furnished their quota; human burial places have been drawn upon; and perhaps most influential of all has been the supposed evidence of loess mussels (*Unionidae*) which really came from Indian mounds! (25, 51, 62)

One reason for this historical reference to the prevailing views mostly of a half-century ago lies in the fact that there is still a tendency in some quarters to exaggerate the abundance, wide distribution, and significance of the freshwater shells which occur in the loess. In numbers they are insignificant when compared with the land forms; they are limited in distribution and practically restricted to what are manifestly pond or slack-water beds; and they are pulmonates which live in shallow waters or at their borders, and may be found in insignificant ponds often on uplands, such as might easily have been buried ultimately in loess dust.

The advocates of water-deposition have been hard put to it to explain the presence of the land shells in the deposit. Kingsmill (33), in his comments on Richthofen's first paper on the loess of China, suggested that "a shell or other animal relic has only to drop into a fissure or be carried down by a stream of water during a flood," and practically the same thought was expressed by Todd somewhat later (66). Un-

fortunately for this view the loess does not fissure sufficiently to admit shells to all parts of the fossiliferous beds, and the shells never appear in vertical seams, but are more likely to show a horizontal arrangement.

It should be noted that the few who have attempted to account for the present condition of the loess by a gradual downward decomposition, as Wood (71), or degradation, as Todd (67), would encounter the same difficulty in accounting for the shells in the loess.

The more common explanation has been that the land shells were washed into the loess-depositing water from adjacent lands, but this view encounters many obstacles.

1. The water-theory postulates either large, persisting lakes, or periodically swollen streams. If the former, then objects as heavy as some of the land shells would not be carried far into the lake, and should be deposited chiefly near its shore. No such shore lines are detectable, nor are the fossils distributed in a way that would suggest either washing into the border of the lake or floating over it as drift,—in the latter case without the accompaniment of silt.

If the latter alternative, the swollen streams, is contemplated then we must consider that to deposit loess in the highest places would require such enormous volumes of water that to expose land surfaces in time for plants and snails to develop powerful currents would be necessary, and these would not be restricted only to the carrying of the fine materials of the loess. The loess is too uniform in texture for this view.

2. Both the vertical and horizontal distribution of the shells in the loess is consistent with that of the modern shells on the surface, and not with that of drifted shells. This has been brought out by the writer in a number of papers (49, 52, 53, 54, 57, 61, 63, 64) and subsequent observations have only served to emphasize the conclusion.

3. If the loess was deposited in water and the land shells were washed into it from higher places, then the loess and the shells should be chiefly on the lower slopes or flats. As a matter of fact, both are most abundant on the highest parts of the ridges in most of the region of well-developed loess.

4. The absence of silt from the inner spire of perfect speci-

mens of loess shells is noteworthy. Fuller and Clapp (27) have objected to this evidence on the ground that this would be included only after prolonged rolling. It is evident that these authors gave little attention to a comparison of land shells carried by running water and those which die and remain on higher ground. Many of the former, especially if submersed, are sure to contain silt, while the latter, like the shells of the loess, will be free from it.

5. *Helicina occulta* is one of the most common and most widely distributed fossils of the loess. Although living on upland wooded slopes, hence terrestrial, it is provided with an operculum. This operculum is drawn a short distance into the body-whorl when the "foot" of the snail is withdrawn into the shell. Not infrequently this operculum is found lying within the body-whorl of fossil specimens. This operculum is detached from the soft parts very soon after the death of the animal, and would not be left within the shell if the latter should be carried by a stream. It is, moreover, of interest to note that in many years' experience the writer has very rarely found drifted modern shells of this species along streams, even where it is locally quite common. The reason for this is probably found in the habits of this snail. It is always found on deeply wooded slopes where the erosional and carrying power of water is slight even during violent storms, and few shells are carried away, even when dead (52, 56, 57).

Fuller and Clapp (27) objected to this evidence and stated that the preservation of the operculum simply means that the shell was buried before the animal decayed. This objection will not stand for three reasons: This snail when living will not float, and a current strong enough to carry it along the bottom would carry coarser material (of which there is always an abundance in the loess region, though not in the loess) than that of the loess; living snails are very rarely washed from the uplands, the empty shells sometimes being carried into the alluvium; and this species particularly (the chief and almost only species to be considered in this connection) rarely finds its way into stream-drift even when dead, as noted above.

As the eolian concept gained ground the remaining advocates

of the aqueous theory (for the most part without first-hand knowledge of the subject) avidly grasped at the misinformation and its consequent misinterpretation beclouded the question even to this day. (For a more detailed discussion of this feature of the subject see the writer's papers, 53, 62, etc.)

Though Richthofen's explanation of the origin of the loess was in disrepute with American geologists, at least so far as American loess was concerned, the writer ventured to present a paper (51) in 1896 in which the origin of the loess was ascribed to eolian agencies. The plausibility of the same explanation was suggested, but not urged, as early as 1890 (49). At that time the writer had not seen Richthofen's papers, and from others had gained the impression that his theory primarily postulated the proximity of large deserts from which the enormous quantities of dust could be derived,—a condition which did not exist in our own country.

This paper was followed by a number of others supplementing and enlarging upon the first (52, 53, 57, 58, 60, 61, 62).

In all the writer's earlier papers the emphasis was placed on the significance of the fauna, though various other, especially physical features were brought out.

Thus it was shown that the loess appears at various altitudes; that in horizontal distribution it is distinctly related to broad stream valleys with large bars at low water, or to sand-dune areas; that along broad valleys it is thicker in the main on the east side; that the particles of which loess is composed are coarser on the east side of the broad valleys; that where lamination is evident it resembles that of dunes rather than of water-deposits; that in practically treeless country the loess is thickest on tops of the ridges, thus resembling snow-drifts formed when the wind is not too strong, but in forested areas it forms a more uniform blanket; that lime-nodules and iron root-tubes may be formed around living roots and are not related to loess-deposition; that there are several interglacial loesses; and other features of minor importance, but related more or less to the genesis of the loess.

Some of these facts had been observed by others, notably those having to do with distribution and structure, but in each case personal observations at least added confirmation.

While the fauna was emphasized its relation to the flora was considered from the first on the basis of personal field-observations, with a growing conviction that the chief value of the mollusks of the loess was as indicators of ecological plant conditions, and this conclusion was presented in several papers, being especially emphasized in "The Genesis of Loess a Problem in Plant Ecology" (60) and in "Land Snails as Indicators of Ecological Conditions" (64).

The value of this molluscan fauna of the loess for purposes of determining climatic and habitat conditions lies in the fact that it consists of species still living³ whose habits and dependence upon living plants are well known. It has been suggested by Kay (32) and others that the fauna was perhaps able to adapt itself to varying climatic conditions of considerable range. This might be true of individual species, but in the light of what is known concerning the habits and distribution of the species composing it, it is inconceivable that the entire fauna could adapt itself to the great changes in climate which would be involved.

The statement (*ibid.*) that "some fossils of the loess have been interpreted as demanding conditions as temperate as the conditions of the present time" should also be corrected, for it is not merely some species but the *entire fauna* which leads to the conclusion stated. It may furthermore be reiterated that there is no warrant for the use of such names as *gelida* (see Baker 2, etc.) for loess forms to express varietal deviation from a type, as there is absolutely no evidence to show that cold was responsible for such deviation.

In 1902 the writer (55) called attention to the three requirements for loess deposition, namely, a source of supply, a transporting agency, and an anchorage for the dust. The first is found in river-bar, sand-dunes, and in lesser degree in any area not closely covered with vegetation. The second is wind, in our territory prevailing from the southwest in summer and the northwest in winter. The third consists of plants

³The recent efforts of F. C. Baker (2, and other papers) to name variants as distinct species or varieties, which then would appear as though extinct, is far-fetched, for these forms are well included within the range of variations shown by the living forms.

which form an unequal covering for the reception of the dust.

Evidence that plants were abundant during loess-deposition is briefly set out in the following four sections:

1. The usually equal or greater thickness of the loess over tops of ridges indicates that during all the period of deposition an anchorage prevented the loose, soft materials of the loess from washing away. Plants alone could furnish such anchorage.

2. The uniform thickness of the loess in many places suggests its deposition in the shelter of taller vegetation,—the forest. The uniform blanket of snow in the forest illustrates the manner of deposition.

3. Abundant root-marks, chiefly in the form of iron-tubules, in many parts of the loess are proof of an abundant vegetation. They are not always in the upper parts of the loess, as Todd (66) tried to show, but they are often buried, under other strata of loess, or even under drift, indicating an earlier vegetation.

The statement of Fuller and Clapp (27) that the perfection of the laminae of the loess shows that they have never been penetrated by rootlets, and hence there were no plants and no food for snails, is without warrant. It is contradicted by the buried root-marks noted above, by the frequent maintenance of fine lamination (a character not always shown by loess) where there is distinct evidence of root penetration, and by the distribution of the shells of herbivorous snails through the deposit which is distinctly not that of drifted shells. The reason for the frequent absence of older root-marks from the upper portions of the loess is evidently due to the modern flora which absorbs the older roots as they decay.

4. The most convincing evidence of the presence of an abundant flora is furnished by the fossil land snails, and they show not only the presence of an abundant vegetation, necessary for food and shelter, but they also indicate floral type areas, as was shown by the writer in various papers (50, 51, 53, 54, 56, 58, 60, 61, 62, and especially 64).

Fuller and Clapp (27) report that in Indiana fossils are found in the loess only up to an altitude of about 500 feet, and they regard this as evidence that water deposited the

loess and shells at lower levels. The true explanation evidently lies in the absence of forests from the higher levels, and the consequent absence of the forest-loving snails. Throughout the Upper Mississippi Valley treeless prairies occupied the more elevated, and hence more exposed areas, and land snails did not thrive upon them.

The question is frequently asked, if vegetation, and especially forest vegetation, was so abundant why do we not find evidences of logs and other vegetable structures? In 1895 the writer (51) made observations near Solon, Iowa, on dust accumulation in the forest during a very dry season, one of several consecutive dry seasons, when an unusually large amount of dust was being transported. A layer of dust approximately 1 mm. in depth covered everything. Some of this was probably blown away again, and other added, but it would probably be a liberal estimate to assume that the net increment was 1 mm. for the season. If a log one foot in diameter lay upon the surface where this increment is being slowly accumulated it would take 300 years to just cover the log if the latter resisted decay. But the log would disappear long before this amount could be accumulated,—and so with all other vegetation. Vegetable structures are preserved only in very wet places, not in the dry situations in which loess is deposited. The same undoubtedly applies to animal remains other than shells of mollusks.

It should be added that the very large iron-tubules (root-marks) which are frequently found in buried loess indicate large roots, probably those of trees.

The foregoing discussion is largely historical, and it is not intended as a criticism of those who held the older views (some of them changed these views as was shown in later papers) but rather as a presentation of the successive steps in the development of this problem.

So long as the aqueous theory of loess-deposition was accepted there were insurmountable difficulties in the way of explaining the ecological conditions under which the land-snail fauna and its concomitant flora could be developed.

The general acceptance of the eolian agency has simplified this part of the problem, as the close connection between cli-

matic conditions, flora and terrestrial molluscan fauna is obvious (64).

For some years, however, the aqueous and eolian agencies have had a rival, more or less insistent, in glacial action, and even where loess was not considered a direct product of the glaciers, efforts have been made to connect its formation with immediate post glacial conditions while the climate was still cold, or at least distinctly cooler than at present (1, 5, 12, 13, 14, 16, 17, 35, 36, 40, 44). Here again the land snails form a barrier which the advocates of glacial or sub-glacial conditions have found it difficult to pass.

In 1879 Todd (66) concluded that because the pond snails of the loess were smaller and few in number the waters were cold, but that, because of the numerous land snails of our present climate, the lands were moist, with their temperature not differing greatly from the present!

A more elaborate effort to show that loess was deposited under near-glacial conditions was made by McGee and Call (40) in 1882. They assumed that the loess was deposited in ice-bound basins or lakes, and supported this in part by the claim that the fauna was depauperate. A plate² is included to show this depauperation, but several significant errors were made. The probability is that the two fossil species of *Limnophysa* do not belong to the species named, and are therefore being compared with modern specimens of different species. Neither the modern nor fossil shells of *Patula striatella* and *Helicina occulta* are of average size, and the difference in the plate is exaggerated. Figures 25-29 are supposed to represent the same species, *Stenotrema monodon*, but figures 28, 29, the two modern shells, represent *S. fraterna*, a much larger species. The figures of *Patula strigosa* similarly exaggerate the difference between fossil and modern forms, for the fossils are much more nearly approached, indeed about equalled, by modern representatives of this extremely variable race. A similar exaggeration appears in the figures of *Succinea obliqua* (now *ovalis*). Figure 35 represents a very large specimen from New York,—much larger than any that the writer has seen

²This plate was drawn by the present writer while a student, though no credit is given for it in the paper. The shells were later destroyed in the mails.

in Iowa. There is, in fact, very little difference between the fossil and modern forms of this species in our territory, especially where the latter come from higher or drier grounds.

This depauperation (so greatly exaggerated in the plate), has been accepted as evidence of a cold climate by a number of authors, and the error has found its way into at least one textbook (25). The writer has repeatedly shown that such depauperation as exists may be traced toward the dry regions of the west, being evidently due to seasonal drouth rather than cold (53, 57, 61).

Many compromises, or combination causes, have been offered, but many of these include deposits other than loess and it is difficult to consider them without taking them up individually. It is sufficient to note that quite a number of these compromises include the condition of a cold climate.

Suffice it to say that the fossils are fatal to every explanation which postulates a climate distinctly colder than the present. Unfortunately, some advocates of a cold climate do not attempt to explain the presence of the shells, but ignore them, or brush them aside as "little shells" of little importance.

The disposition to connect the formation of loess closely with glacial conditions is probably due in large part to the common linking of loess with the Iowan Drift. Calvin (13, 15) observed that there is quite an accumulation of loess just outside the Iowan border in Iowa, and the same observation has been made in Illinois since.

Unfortunately, the conclusions based on a rather limited area have been applied to the entire loess field. The two greatest areas of loess-deposition are found in western Iowa, along the Missouri, and in central Nebraska, along the Platte.

In the Iowa field the loess is thickest in the bluffs bordering the valley of the Missouri, and tapers down to a comparatively thin deposit near the border of the Wisconsin Drift in Carroll County. It here probably approaches close to the old buried ~~border~~ of the Iowan, but by its thin edge,—the great bulk lies quite a distance to the southwest and west. If there was any connection between this greatest of our loess deposits and the Iowan it might be expected that the bulk of it would

be nearer the Iowan instead of the reverse. Its evident source is shown in Plate I, Fig. 1.

Even more convincing is the loess of central and southern Nebraska, which has received so little attention from students of the problem. It was mentioned by Todd (66), but Savage (48) in a paper which admirably sets out certain phases of the loess problem, errs in stating that loess extends only a few miles west of the Missouri. The writer has found typical fossiliferous loess not only at Lincoln, Platte River Junction, Abie, Hooper, Bremer, West Point, and Clarkson, all localities well back from the Missouri River, but also at North Platte in central Nebraska, along the Platte River, and at Oxford and Atlanta in the south-central part of the state, along the Republican River. The manifest source of the material is shown in Plate I, Figs. 2 and 3.

The deposit along the Platte is much bulkier than that along the border of the Iowan in Iowa, and that along the Republican quite equals it. Yet it would be very difficult to establish any connection between these deposits and the Iowan Drift, while the relation to the broad bars of the Platte and the Republican is obvious.

It is interesting to note that of the 2130 fossils which the writer collected in the North Platte and Republican areas, the great majority, or 1972, belong to the species *Vallonia gracilicosta*, *Gonyodiscus shimekii*, *Pupilla muscorum*, *Succinea grosvenorii*, and *Succinea avara*, these and the remaining species all occurring also in the loess of Iowa.

With the exception of the widely distributed *Succinea avara*, the remaining species named look westward for their modern prototypes, though the *Vallonia* and *Succinea grosvenorii* still live in Iowa, the latter only in the western part.

The southern loess also fails to connect definitely with the Iowan, and that is especially true of that which lies west of the lower Mississippi, as on Crowley's Ridge, Arkansas. It is possible that some of the material might have been washed down from the Iowan Drift in the north, but it is probable that the bulk of the northern contribution came from the massive deposit along the Missouri to which reference is made above.

There seems to be no adequate reason for the wholesale linking of the bulk of the loess with the Iowan, and there is certainly no warrant for the belief that loess was deposited in a cold climate (49, 56, 57, 59, 61).

On the contrary, it is more likely that loess deposition did not begin until the glacial ice retreated far to the north. After the recession of each glacial sheet the area from which it retreated was soon covered with a swamp and prairie vegetation such as covered the Wisconsin Drift lobe in Iowa before its settlement. The streams were sluggish, few bars were formed or exposed, there were many kettleholes (see Plate II, Figure 3), and the dust supply was limited. A long period of time would be required to cut and widen the river-channels so that extensive bars would be formed, the ice in the meantime retreating far beyond the loess territory. This period of time would be longest in the case of the Kansan (which even today has not finished this process in northwestern Iowa, see Plate II, Fig. 2, and in more limited areas in the southern part) because it covered the entire state, during which important changes occurred in the Kansan itself, and it would be correspondingly shorter for the drift sheets which only partly covered the state (see Plate II, Figs. 1 and 3), since the deeply eroded Kansan offered readier drainage-outlets.

The loess, instead of being closely connected with the ice sheets, was evidently widely separated from them in time.

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PLATE I



Figure 1



Figure 2



Figure 3

EXPLANATION OF PLATE I

Little Eroded Drift Surface From Which Little Dust Is Derived—
Originally Prairie

Fig. 1—A bar consisting of sand and fine yellow silt, along the Missouri River, Harrison County, Iowa. The valley is bordered with loess bluffs.

Fig. 2—Bars in the Platte River at North Platte. Loess bluffs border the south side of the river.

Fig. 3—Bars in the Republican River near Oxford, Nebraska. Loess bluffs border the valley.

PLATE II



Figure 1



Figure 2

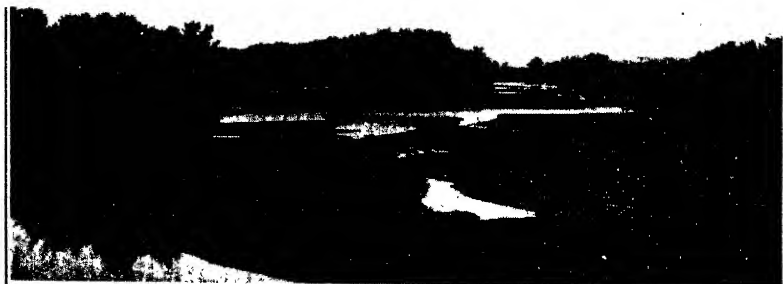


Figure 3

EXPLANATION OF PLATE II

River-bars, the Source of Loess Dust

Fig. 1—Iowan drift in Bremer County, Iowa.

Fig. 2—Kansan drift in O'Brien County, Iowa.

Fig. 3—Morainic Wisconsin drift surface, with two kettleholes.

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UNIVERSITY OF IOWA STUDIES IN NATURAL HISTORY

HENRY FREDERICK WICKHAM, Editor

Volume XIV

Number 3

The Mechanical Composition of Sediments in Graphic Form

by

CHESTER K. WENTWORTH

Published by the University, Iowa City, Iowa

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The Mechanical Composition of Sediments in Graphic Form

CHESTER K. WENTWORTH

INTRODUCTION

It is now about ten years since the writer, through his association with T. W. Vaughan and E. W. Shaw, then of the United States Geological Survey, came into contact with the problems connected with the mechanical composition of sediments. At that time, as a part of an increasing interest in America in the critical study of sediments, the matter of standard sieve scales and uniform conventions of plotting was under consideration and the writer first became aware of the very great variety of schemes of analysis and forms of plotting which had been and to a considerable extent still is a serious impediment to the comparison and interpretation of mechanical sediments.

Among the several grade scales in use, the one best fitted for general use by geologists appeared to be the 1-2-4-8 millimeter scale and this was adopted at that time by the writer and several of his associates engaged in studies of sediments. In addition to the advantages of simplicity and rational development possessed by this scale there was a powerful argument for its adoption in the very important pioneer work of Udden which had been done in accordance with it. Discussion of the specific advantages of the 1-2-4-8 millimeter scale has been presented elsewhere and need not be repeated.¹ Within the past few years there has been a growing adherence to it by students engaged in the study of mechanical composition and it was adopted by W. H. Twenhofel as the standard scale for the *Treatise on Sedimentation*. On the other hand there continue to appear contributions by in-

¹Wentworth, C. K., A Scale of Grade and Class Terms for Clastic Sediments, *Jour. of Geol.*, Vol. 30, pp. 381-382, 1922. *Methods of Mechanical Analysis of Sediments*, U. of Iowa Studies in Nat. History, Vol. XI, No. 11, pp. 21-25, 1926. A Method of Computing Mechanical Composition Types in Sediments, *Geol. Soc. Amer. Bull.* 40, pp. 771-790, 1929.

investigators who have used the Bureau of Soils scale or the Tyler Standard scale, usually because of slightly greater ease in securing sieves. Still more unfortunate is the occasional publication of papers in which the sieves are designated by the number of meshes to the inch and in which no data as to size of opening are given.

In view of these facts continued advocacy and wider discussion appear to be needed and the following compilation of analyses in graphic form is presented to that end. It was intended originally to collect 1000 analyses and there is little doubt that more than that number of analyses of sediments of known origin have been made. However, the pressure of other projects, and the considerable delay already incurred, which it seems unwise to prolong, lead the writer to present the collection as it stands with the hope that others will supplement it as additional studies are made.

The principal utility of a collection such as this is to enable students to see the various types of mechanical composition more vividly than is possible in numerical tables and to offer a somewhat comprehensive guide for the interpretation of origin of sediments in which the mechanical composition appears to be distinctive. As the writer has pointed out elsewhere² a very large amount of critical study is needed before the mechanical composition of sediments can be used in a broadly diagnostic way in the solution of genetic problems. It is thought that the most effective means to progress in this field consists of extended statistical analyses of the mechanical composition data considered as frequency distributions and in the paper cited a comparatively simple computing procedure has been described. It is sufficient to state here that in this procedure values for the *Mean Size*, *Standard Size Ratio Deviation* (a measure of degree of sorting), and *Skewness* (Asymmetry) are derived which indicate in numerical form the chief characteristics of the curve of frequency distribution and which greatly facilitate averaging, plotting and other manipulations of these data.

It is believed that the present compilation will enable stu-

²Wentworth, C. K., A Method of Computing Mechanical Composition Types in Sediments, Geol. Soc. Amer. Bull. 40, pp. 771-790, 1929.

dents to select sediments showing mechanical composition of certain general required characteristics or due to a particular agent or set of conditions to which the computing procedure mentioned above may be applied for detailed comparison and study. It is thought that in this way only will accurate data be obtained on the grade distance between the mean values for the two maxima of certain double maximum sediments like river gravels or between the mean sizes of grains of different densities in a complex sand. It is thought, moreover, that within these characteristics of sorting by the two fluids, air and water, with their variations in velocities and other conditions of transport, are contained some very fundamental facts, which a sufficiently searching study will bring out to the great furtherance of interpretive studies.

SOURCE AND ARRANGEMENT OF DATA

For the most part analyses portrayed here were made to the 1-2-4-8 millimeter scale. In a few instances, as indicated in the references below, analyses made to another scale have been converted to the standard scale by the writer. The converted portions commonly have an unavoidable smoothness in the region not so completely covered by the data of the analysis.

In the interest of brevity and economy of space the source information for each pyramid or histogram representing an analysis has been conventionalized. For example, in (Figure 46 (I—235) Dune sand, Nebraska), the serial number for this publication is 46, the Roman numeral I refers to the list below and indicates the paper by J. A. Udden and the number 235 is the original one used by Udden. The name following the parenthesis in most cases is that given by the author or analyst, though in a few instances it has been changed by the present writer to better describe the material. Only in a few instances has the most important data concerning the situation of collection been given and the locality has been simplified to the name of the state or other such general region.

Graphic presentation is naturally of limited accuracy. There are those who will object that significant computations can

only be made from data in which the fractions of percentages are given. The writer has discussed this question elsewhere³ and believes that at the present stage of studies in this field and with the uncertainty attending the collecting of samples the graphic data here presented are as accurate as can readily be utilized and that computations made from them with readings to the nearest 1% will yield frequency constants quite as precise as are justified by the original conditions of collecting and analysis.

In the figures which follow the sediments have been arranged under the main genetic headings and under lesser headings in as logical manner as seemed practicable. In a few instances groups of sediments analyzed by one person in a series have been kept together though not strictly of the same sort. An effort has been made to arrange the material in the way most likely to prove useful. Somewhat arbitrary classifications have been made by the writer in places and in case of doubt or desire to make selections for a special purpose the reader is referred to the original published data.

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PLATE I

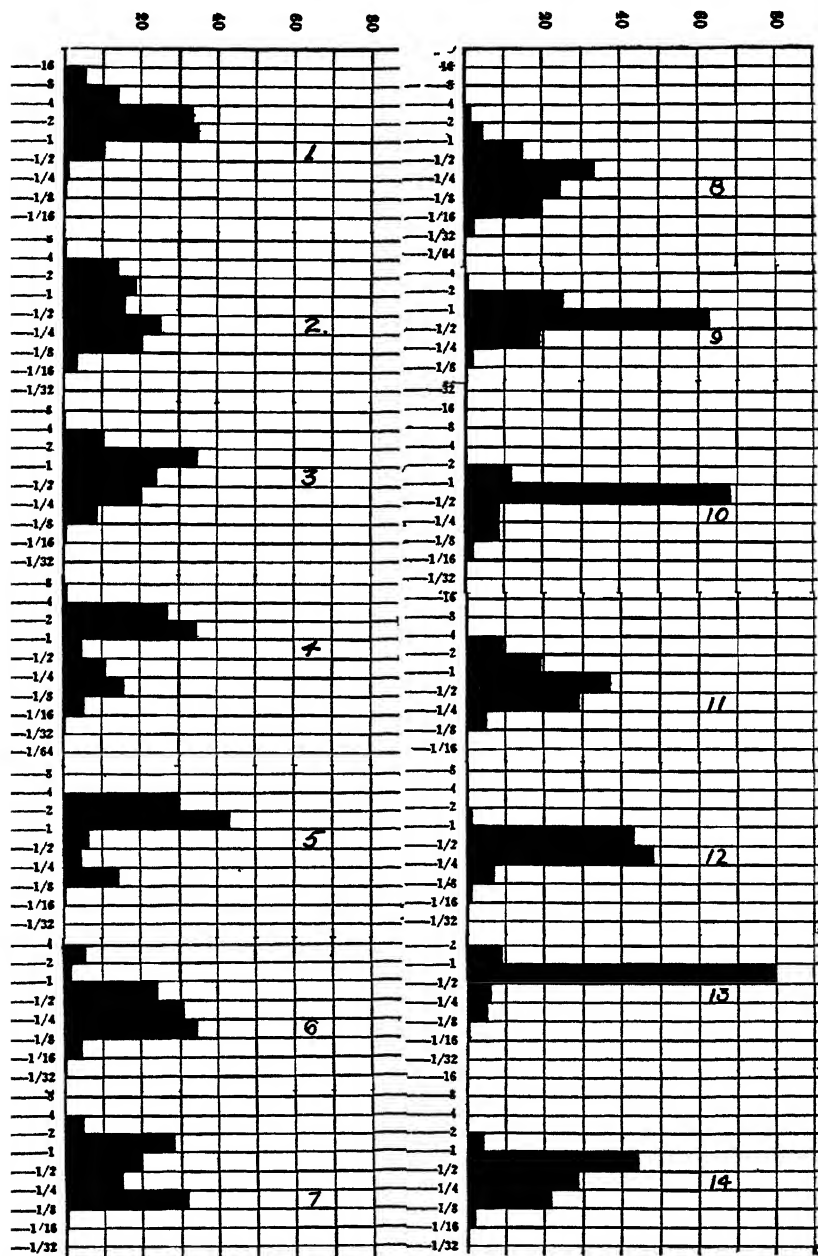
EOLIAN SEDIMENTS

Lag Gravel

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Figure 3 (I—193) Lag gravel, from "blowout," Illinois.
Figure 4 (I—194) Lag gravel, Illinois.
Figure 5 (I—195) Lag gravel, rear of dune, Indiana.
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Figure 11 (XI—2065) Eolian lag sand, Virginia.
Figure 12 (XI—2074C) Eolian lag sand, Virginia.

Coarse Drifting Sand

- Figure 13 (I—201) Drift sand, rear dune slope, Nebraska.
Figure 14 (I—202) Drift sand, rear dune slope, Illinois.



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PLATE II

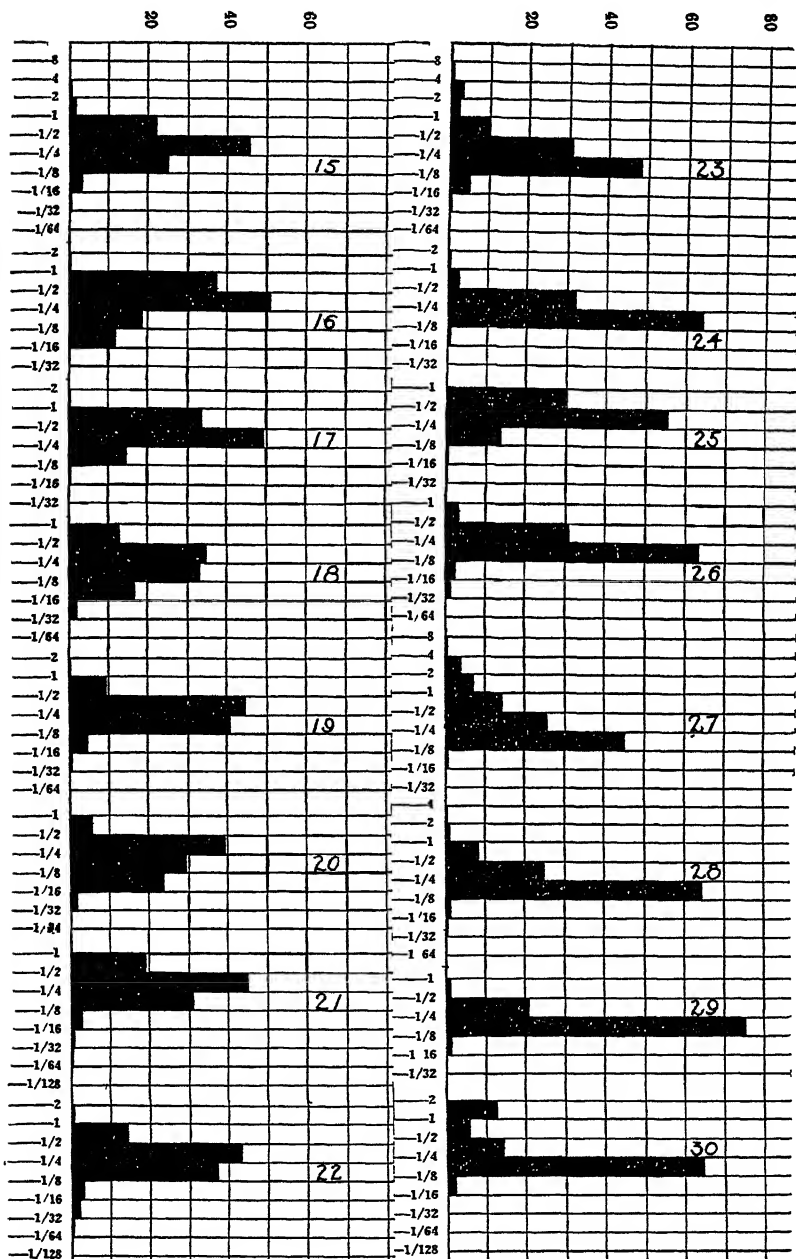
EOLIAN SEDIMENTS

Coarse Drifting Sand

- Figure 15 (I—203) Drift sand, rear dune slope, Illinois.
Figure 16 (I—204) Drift sand, rear dune slope, Nebraska.
Figure 17 (I—205) Drift sand, rear dune slope, Nebraska.
Figure 18 (I—206) Drift sand, rear dune slope, Illinois.
Figure 19 (I—207) Drift sand, rear dune slope, Illinois.
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Dune Sand

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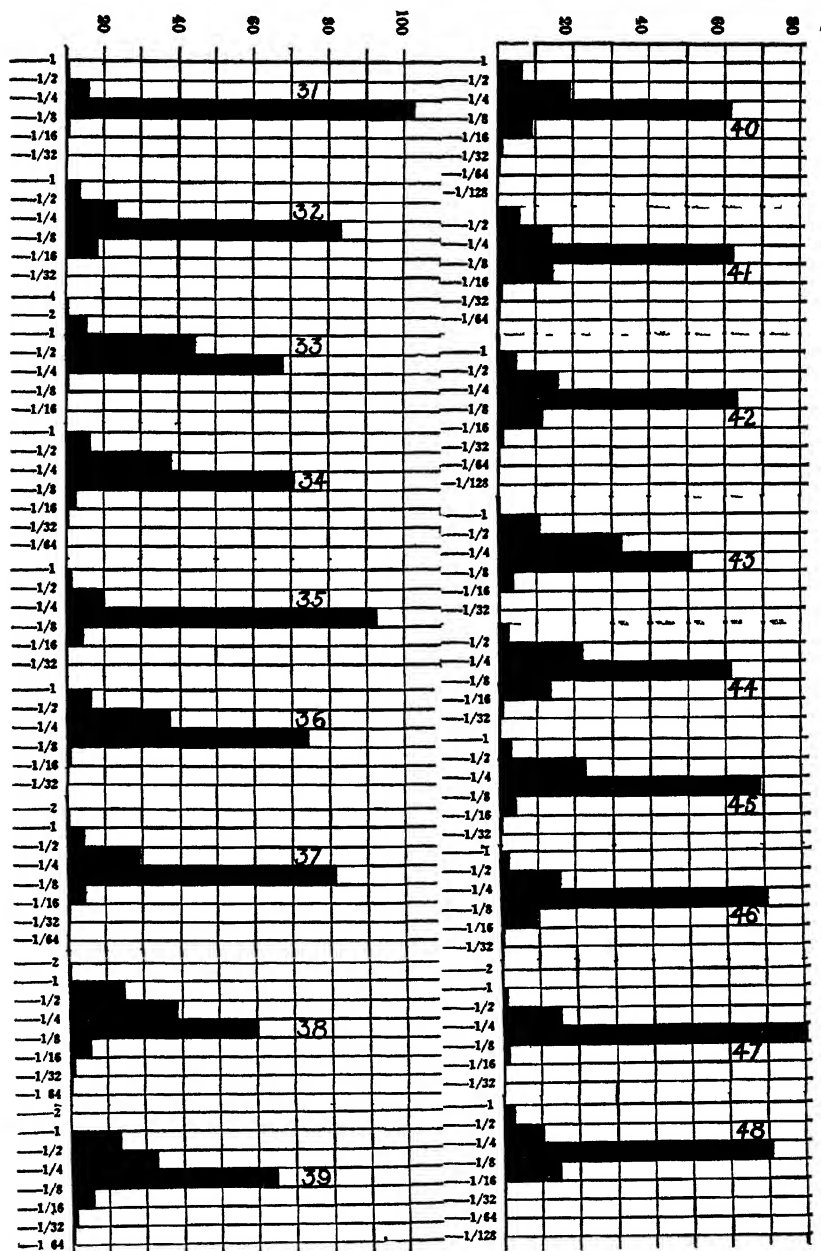
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EOLIAN SEDIMENTS

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Figure 42 (I—231) Blown sand, North Dakota.
Figure 43 (I—232) Dune sand, Illinois.
Figure 44 (I—233) Dune sand, Illinois.
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Figure 46 (I—235) Dune sand, Nebraska.
Figure 47 (I—236) Dune sand, front slope, Nebraska.
Figure 48 (I—237) Dune sand, from coarse layer, Nebraska.



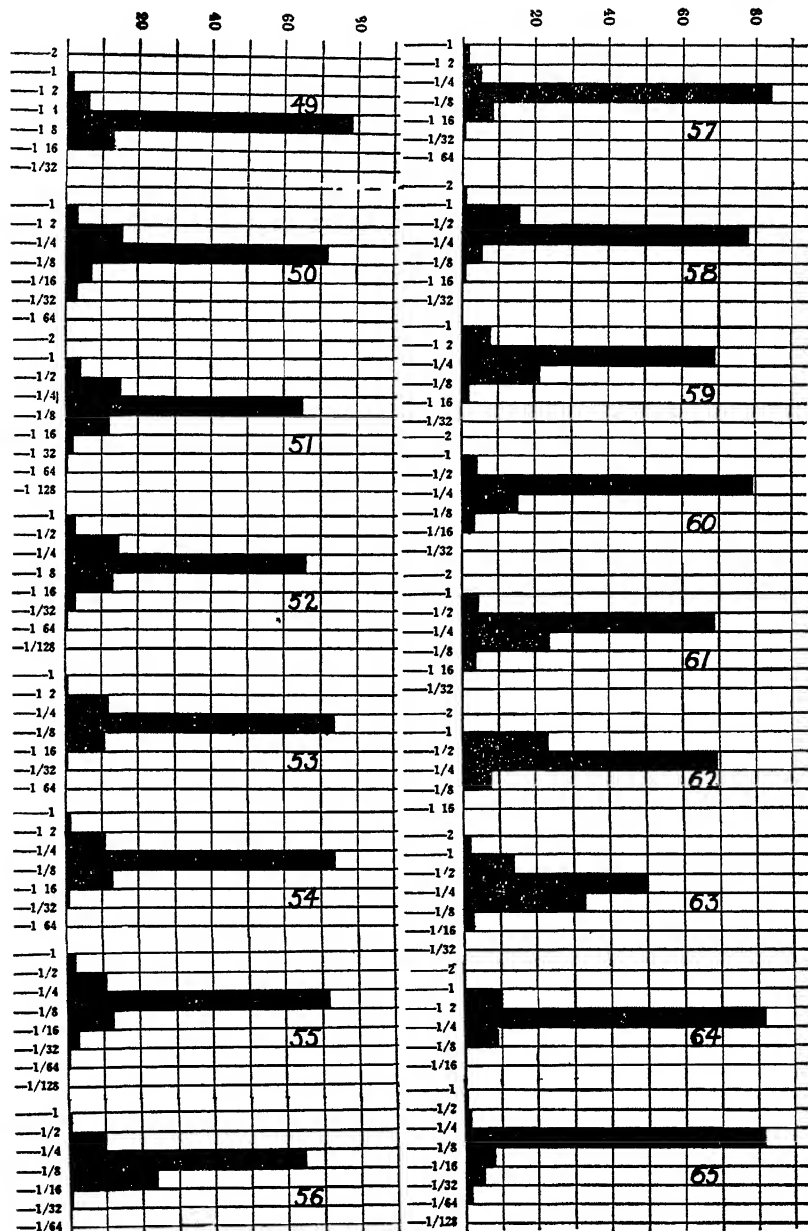
Figures 31-48

PLATE IV

EOLIAN SEDIMENTS

Dune Sand

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Figure 59 (XI—2072B) Dune sand, Virginia (See beach sand
XI—2072A).
Figure 60 (XI—2074A) Dune sand, Virginia.
Figure 61 (XI—2074B) Dune sand, Virginia.
Figure 62 (XI—2076) Dune sand, Virginia.
Figure 63 (VIII—216) River dune sand, Georgia.
Figure 64 (XI—2063) Dune sand, Virginia.
Incipiently Blown Sand
Figure 65 (I—248) Blown sand, field, Illinois.



Figures 49-65

PLATE V

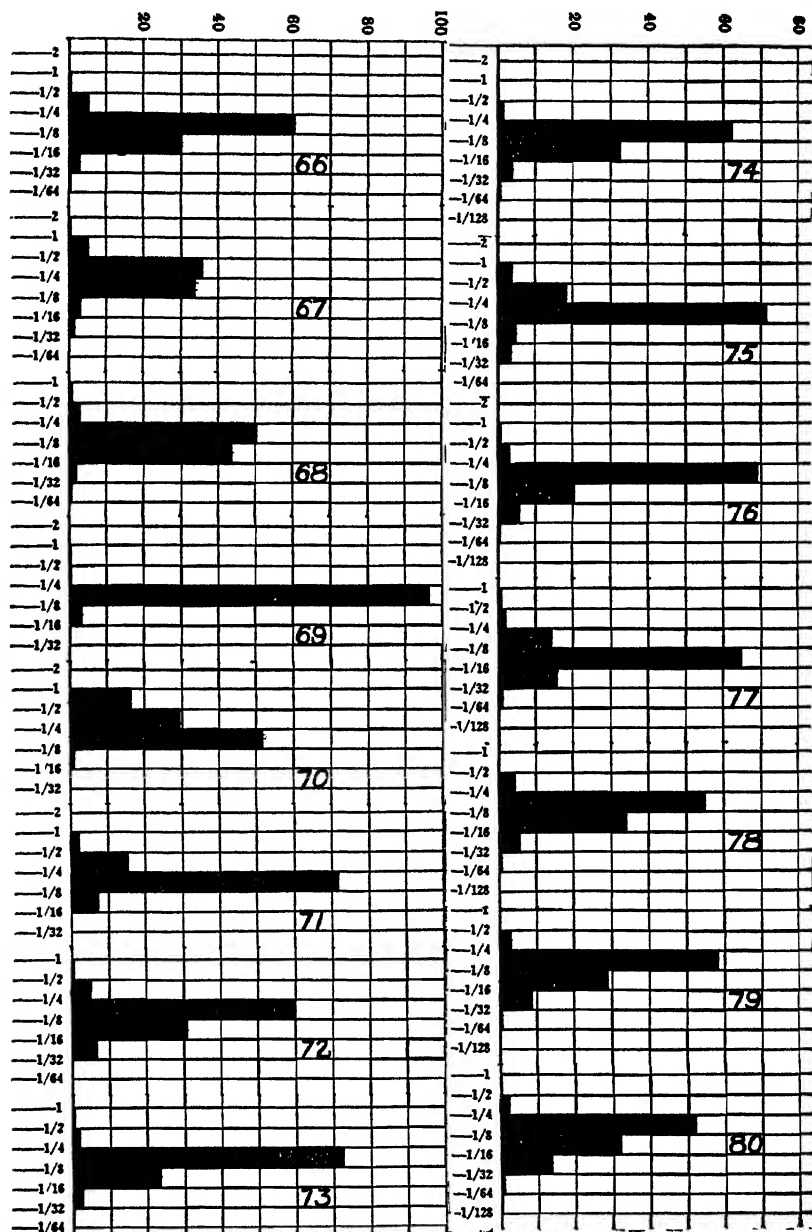
EOLIAN SEDIMENTS

Incipiently Blown Sand

- Figure 66 (I—249) Blown sand, Kansas.
Figure 67 (I—250) Blown sand, snow drift, Maryland.
Figure 68 (I—251) Blown sand, gutter, Maryland.
Figure 69 (I—252) Blown sand, beach, Florida.
Figure 70 (I—253) Blown sand, railroad bed, Illinois.

Lee Sand

- Figure 71 (I—254) Lee sand, Kansas.
Figure 72 (I—255) Lee sand, six feet in front of lee drift, Kansas.
Figure 73 (I—256) Lee sand, fifteen feet in front of lee drift, Kansas.
Figure 74 (I—257) Lee sand, twenty-four feet in front of lee drift, Kansas.
Figure 75 (I—258) Lee sand, from lee drift, Kansas.
Figure 76 (I—259) Lee sand, ten feet ahead of lee drift, Kansas.
Figure 77 (I—260) Lee sand, fifty feet ahead of lee drift, Kansas.
Figure 78 (I—261) Lee sand, ten feet ahead of small dune, Illinois.
Figure 79 (I—262) Lee sand, 100 feet ahead of small dune, Illinois.
Figure 80 (I—263) Lee sand, 160 feet ahead of small dune, Illinois.



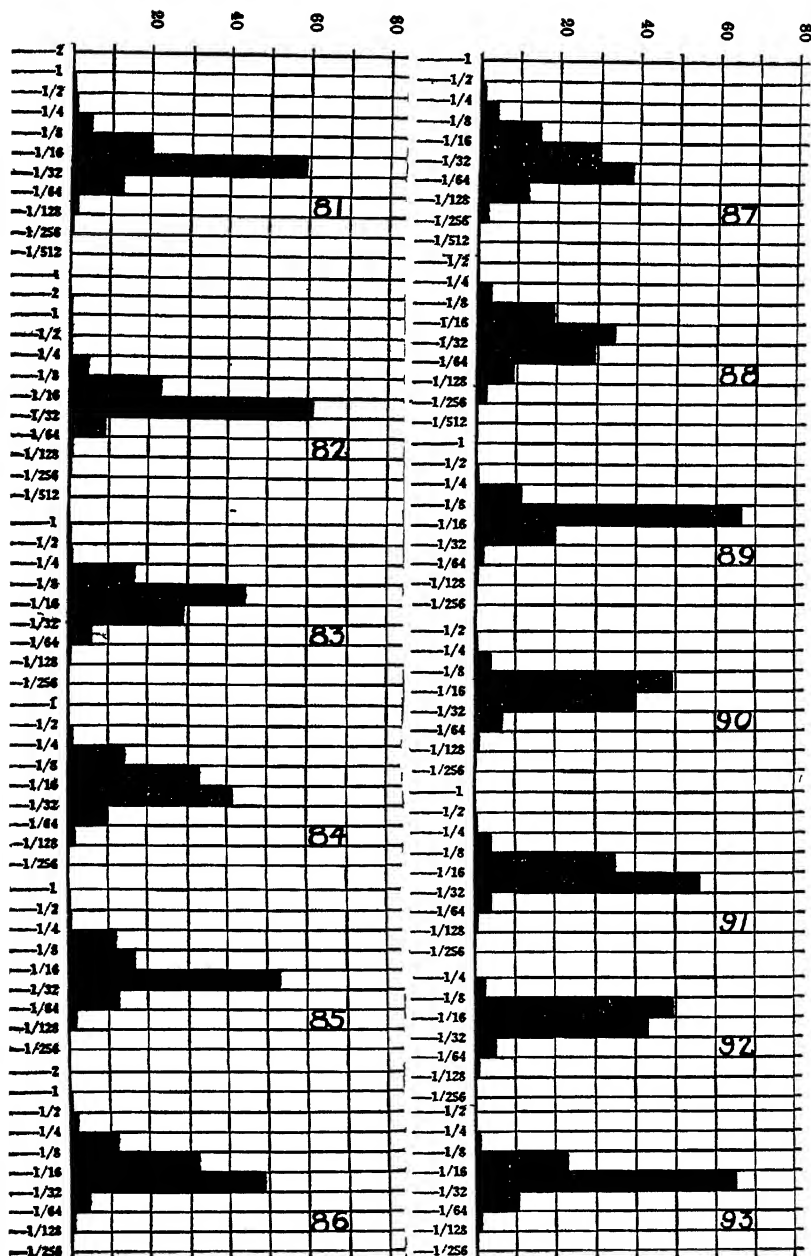
Figures 66-80

PLATE VI

EOLIAN SEDIMENTS

Miscellaneous Types of Dust

- Figure 81 (I—264) Dust, in house four miles from blown field, North Dakota.
- Figure 82 (I—265) Dust, in house four miles from blown field, North Dakota.
- Figure 83 (I—266) Dust, from running railway coach, Arizona.
- Figure 84 (I—267) Dust, from running railway coach, Minnesota.
- Figure 85 (I—268) Dust, from running railway coach, Nebraska and Kansas.
- Figure 86 (I—269) Dust, from running railway coach, New England.
- Figure 87 (I—270) Dust, from running railway coach, North Dakota and Montana
- Figure 88 (I—271) Dust, from running railway coach, Northwest United States.
- Figure 89 (I—272) Dust, from running railway coach, Utah.
- Figure 90 (I—273) Dust, from running railway coach, North Dakota.
- Figure 91 (I—274) Dust, from running railway coach, North Dakota.
- Figure 92 (I—275) Dust, from running railway coach, Minnesota.
- Figure 93 (I—276) Dust, from running railway coach, Colorado.



Figures 81-93

PLATE VII

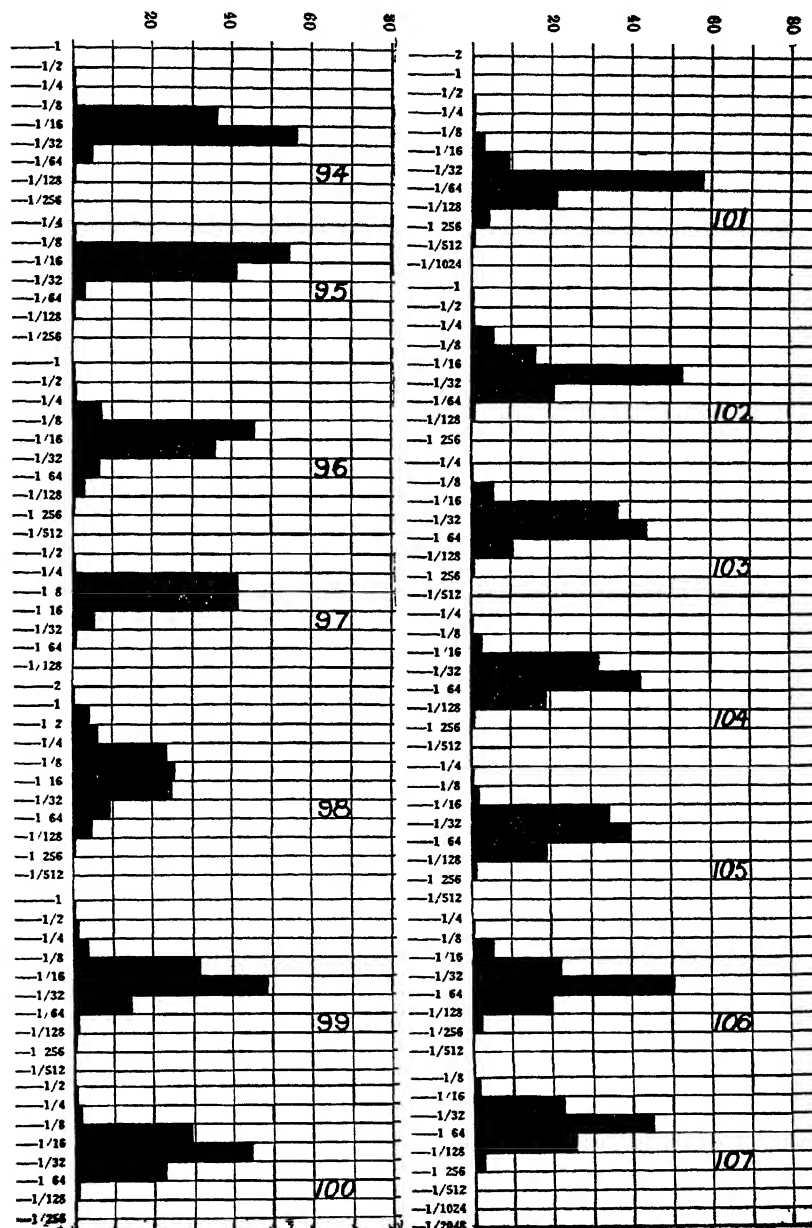
EOLIAN SEDIMENTS

Miscellaneous Types of Dust

- Figure 94 (I—277) Dust, from running railway coach, Kansas.
- Figure 95 (I—278) Dust, from running railway coach, Northwest United States.
- Figure 96 (I—279) Dust, window sill, Arizona.
- Figure 97 (I—280) Dust, volcanic, from snow, Norway.
- Figure 98 (I—281) Dust, five feet from road, Maryland.
- Figure 99 (I—282) Dust, fifteen feet from road, Maryland.
- Figure 100 (I—283) Dust, twenty-five feet from road, Illinois.
- Figure 101 (I—284) Dust, twenty-five feet from road, Maryland.
- Figure 102 (I—285) Dust, from ice, Minnesota.

Dust from Known Winds

- Figure 103 (I—286) Dust, wind under nine miles per hour.
- Figure 104 (I—287) Dust, wind under ten miles per hour.
- Figure 105 (I—289) Dust, wind under 13 miles per hour.
- Figure 106 (I—290) Dust, wind under 19 miles per hour.
- Figure 107 (I—291) Dust, wind under 22 miles per hour.



Figures 94-107

PLATE VIII

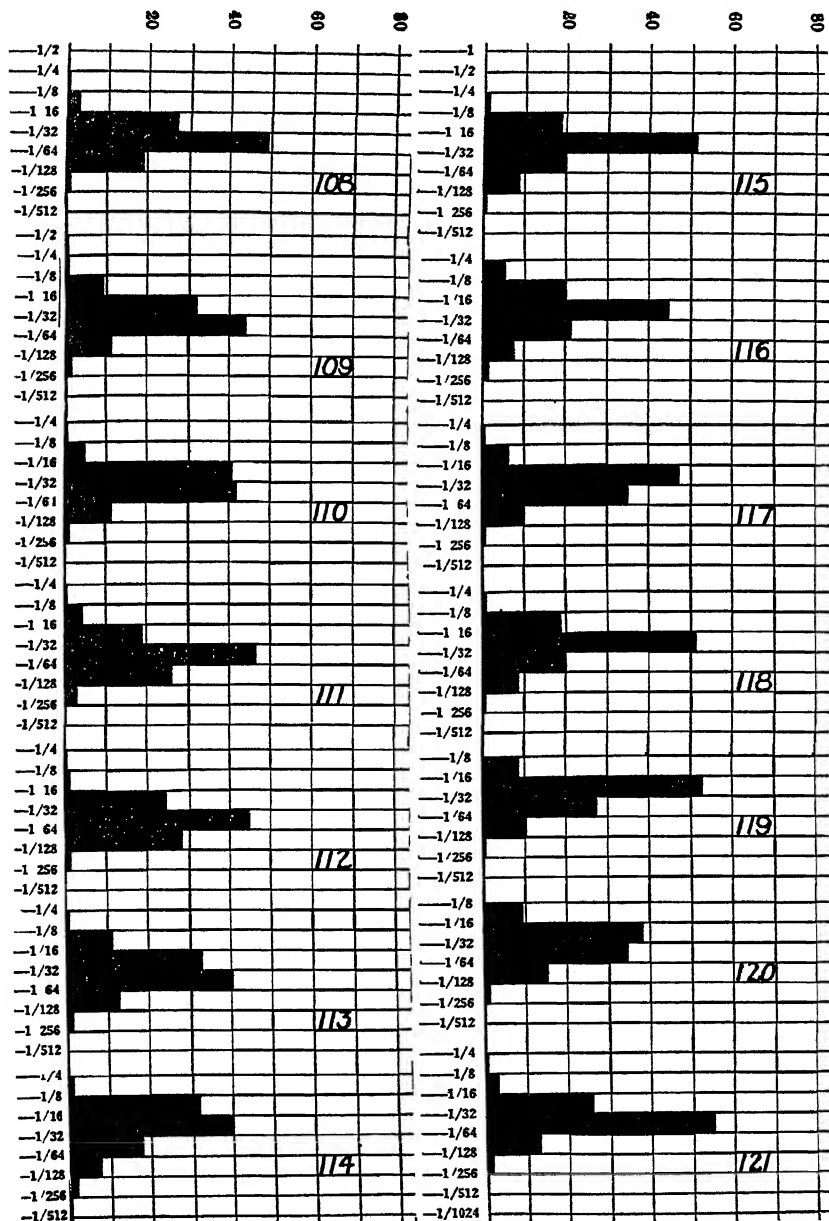
EOLIAN SEDIMENTS

Dust from Known Winds

- Figure 108 (I—292) Dust, wind under 22 miles per hour.
Figure 109 (I—293) Dust, from air ninety feet above ground.
Figure 110 (I—294) Dust, from air ten feet above ground.
Figure 111 (I—295) Dust, top flagpole.
Figure 112 (I—296) Dust, near ground.
Figure 113 (I—297) Dust, wind under 14 miles per hour.
Figure 114 (I—298) Dust, wind under 18 miles per hour.
Figure 115 (I—299) Dust, wind under 18 miles per hour.
Figure 116 (I—300) Dust, wind under 19 miles per hour.
Figure 117 (I—301) Dust, wind under 20 miles per hour.
Figure 118 (I—302) Dust, wind under 21 miles per hour.
Figure 119 (I—303) Dust, wind under 23 miles per hour.
Figure 120 (I—304) Dust, wind under 24 miles per hour.
Figure 121 (I—305) Dust, from air ten feet above ground.

MECHANICAL COMPOSITION OF SEDIMENTS 25

Plate VIII



Figures 108-121

PLATE IX

EOLIAN SEDIMENTS

Dust from Surfaces Above the Ground (Taken chiefly from
the leaves and branches of trees in Illinois)

Figure 122 (I—306) Dust.

Figure 123 (I—307) Dust.

Figure 124 (I—308) Dust.

Figure 125 (I—309) Dust.

Figure 126 (I—310) Dust.

Figure 127 (I—311) Dust.

Figure 128 (I—312) Dust.

Figure 129 (I—313) Dust.

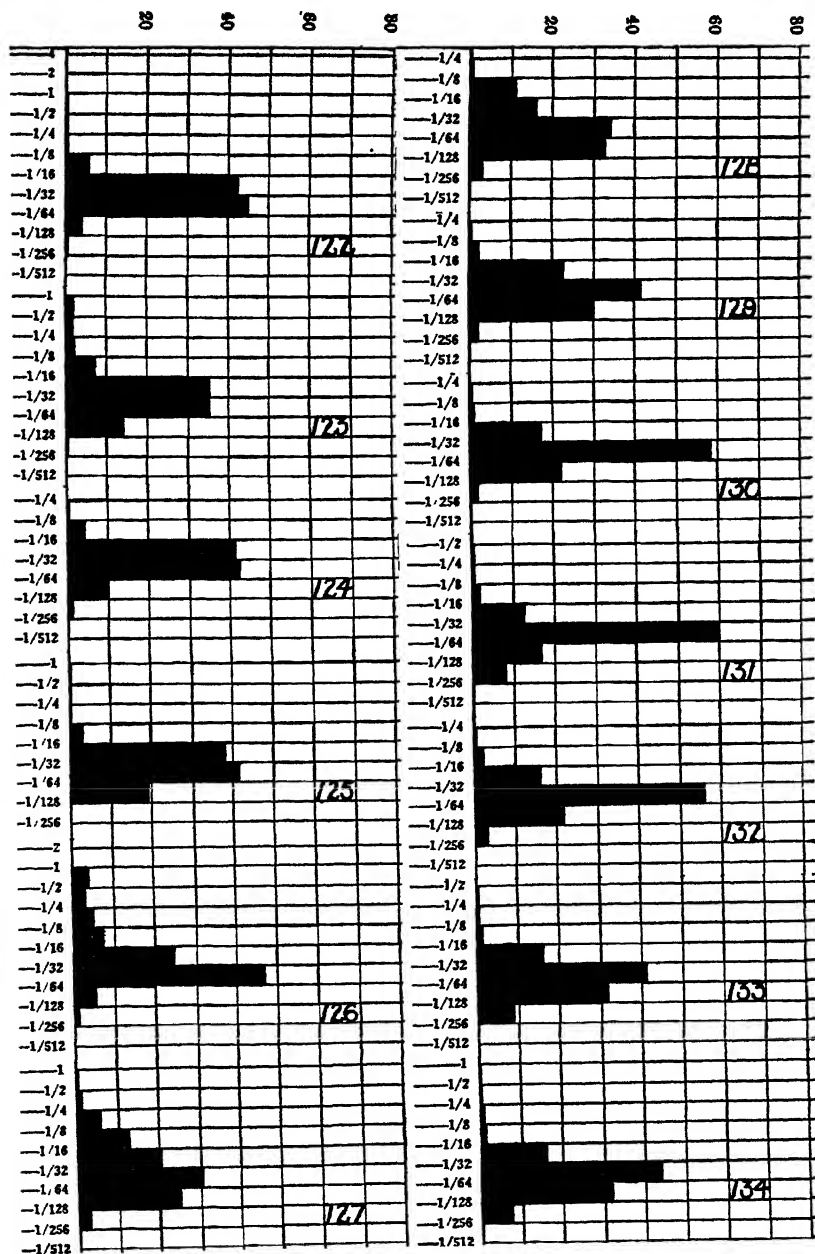
Figure 130 (I—314) Dust.

Figure 131 (I—315) Dust.

Figure 132 (I—316) Dust.

Figure 133 (I—317) Dust.

Figure 134 (I—318) Dust.



Figures 122-134

PLATE X

EOLIAN SEDIMENTS

Dust from Surfaces Above the Ground (Taken chiefly from
the leaves and branches of trees in Illinois)

Figure 135 (I—319) Dust.

Shower Dust

Figure 136 (I—320) Shower dust, Missouri.

Figure 137 (I—321) Shower dust, Iowa.

Figure 138 (I—322) Shower dust, Iowa.

Figure 139 (I—323) Shower dust, Illinois.

Figure 140 (I—324) Shower dust, Illinois.

Figure 141 (I—325) Shower dust, Illinois.

Figure 142 (I—326) Shower dust, Illinois.

Figure 143 (I—327) Shower dust, Illinois.

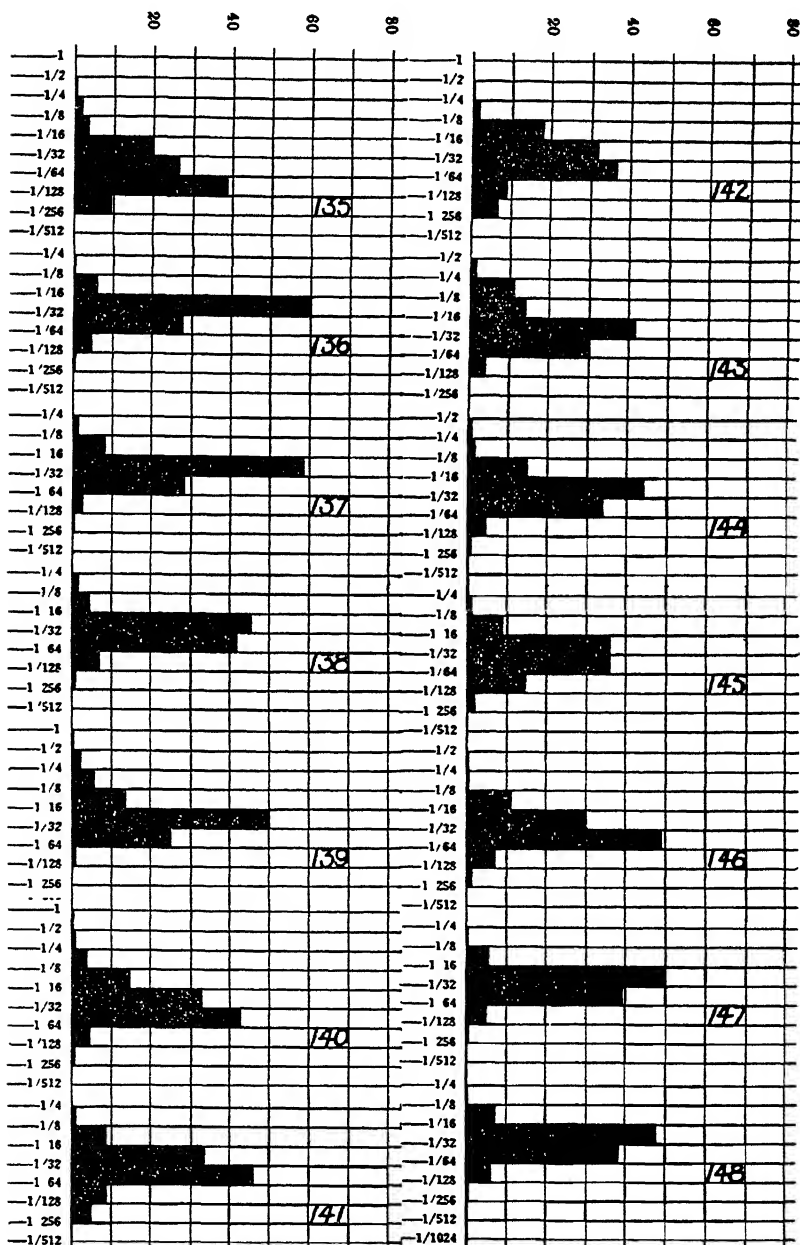
Figure 144 (I—328) Shower dust, Illinois.

Figure 145 (I—329) Shower dust, Illinois.

Figure 146 (I—330) Shower dust, Illinois.

Figure 147 (I—331) Shower dust, Illinois.

Figure 148 (I—332) Shower dust, Illinois.



Figures 135-148

PLATE XI

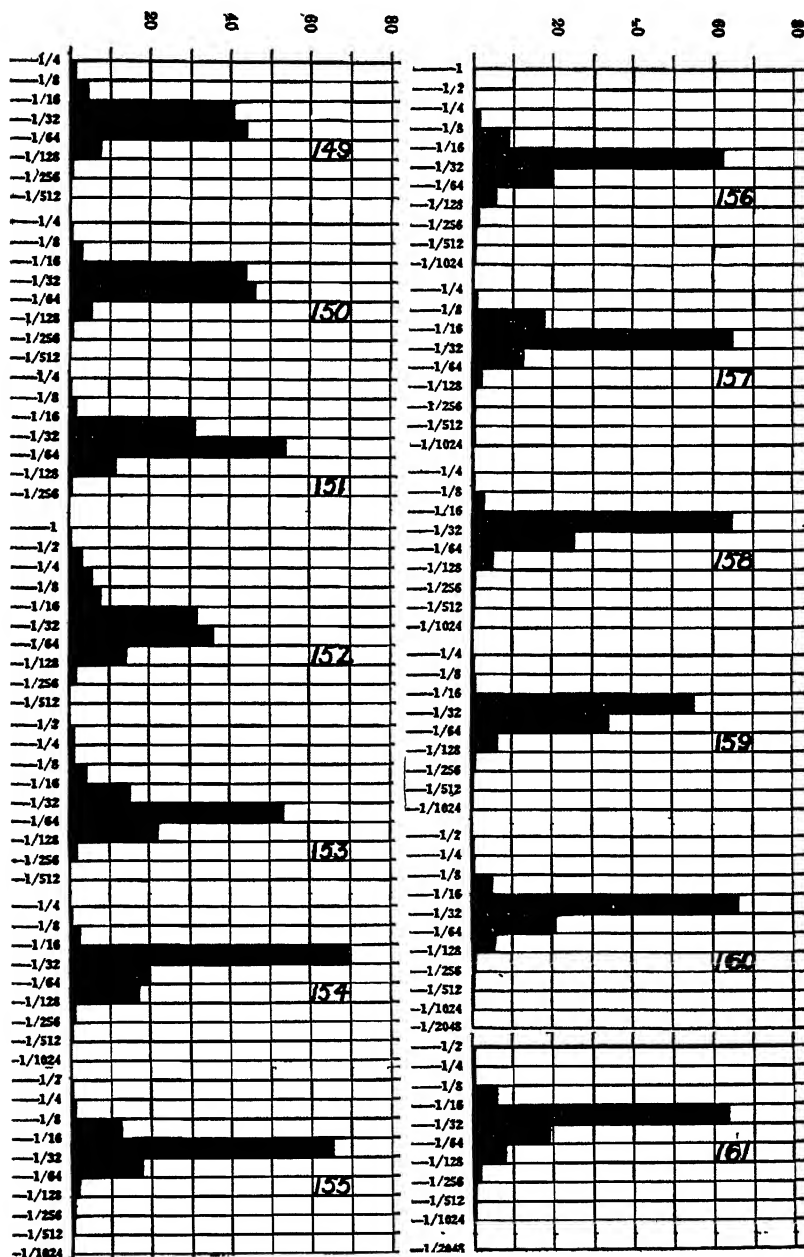
EOLIAN SEDIMENTS

Shower Dust

- Figure 149 (I—333) Shower dust, Illinois.
Figure 150 (I—334) Shower dust, Illinois.
Figure 151 (I—335) Shower dust, Illinois.
Figure 152 (I—336) Shower dust, Illinois.
Figure 153 (I—337) Shower dust, New York.

Loess

- Figure 154 (I—352) Loess, Iowa.
Figure 155 (I—353) Loess, near base, Iowa.
Figure 156 (I—354) Loess, twenty feet above base, Iowa.
Figure 157 (I—355) Loess, forty feet above base, Iowa.
Figure 158 (I—356) Loess, sixty feet above base, Iowa.
Figure 159 (I—357) Loess, twenty feet below top, Iowa.
Figure 160 (I—358) Loess, fifteen feet below top, Iowa.
Figure 161 (I—359) Loess, eight feet below top, Iowa.



Figures 149-161

PLATE XII

EOLIAN AND FLUVIAL SEDIMENTS

Loess and River Gravel

Figure 162 (I—360) Loess, two feet below top. Iowa.

Figure 163 (I—361) Loess, ten inches below top, Iowa.

Figure 164 (I—362) Loess, top soil, Iowa.

FLUVIAL SEDIMENTS

River Gravel

Figure 165 (I—74) River gravel, Iowa.

Figure 166 (I—75) River gravel, Alaska.

Figure 167 (I—76) River gravel, Alaska.

Figure 168 (I—77) River gravel, Alaska.

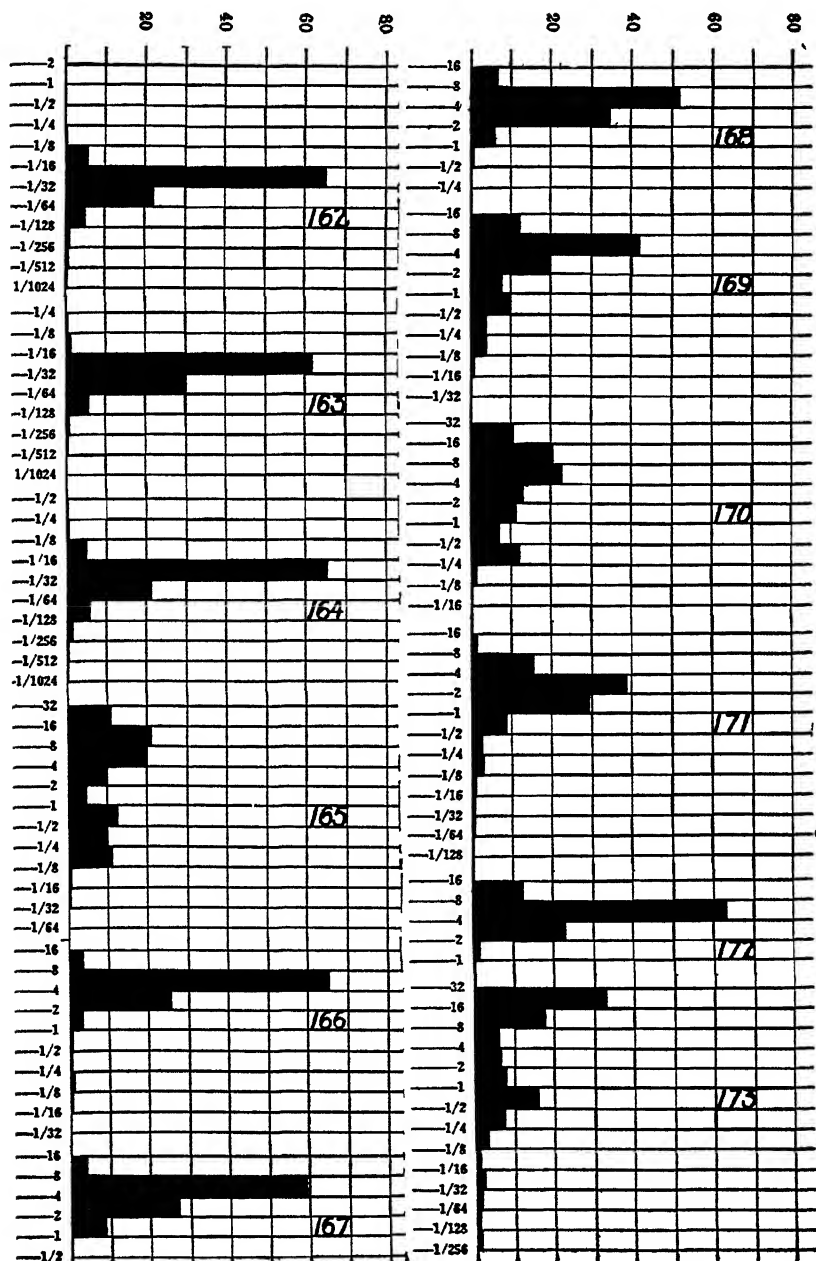
Figure 169 (I—78) River gravel, Alaska.

Figure 170 (I—79) River gravel, Alaska.

Figure 171 (I—80) River gravel, Iowa.

Figure 172 (II—79) River gravel, Virginia.

Figure 173 (II—558) River gravel, Virginia.



Figures 162-173

PLATE XIII

FLUVIAL SEDIMENTS

River Gravel

Figure 174 (VII—31-954A) Stream gravel, California.

Creek Gravel

Figure 175 (I—56) Creek gravel, Texas.

Figure 176 (I—57) Creek gravel, Texas.

Figure 177 (I—58) Creek gravel, Iowa.

Figure 178 (I—60) Creek gravel, Iowa.

Figure 179 (VIII—145) Creek gravel, Georgia

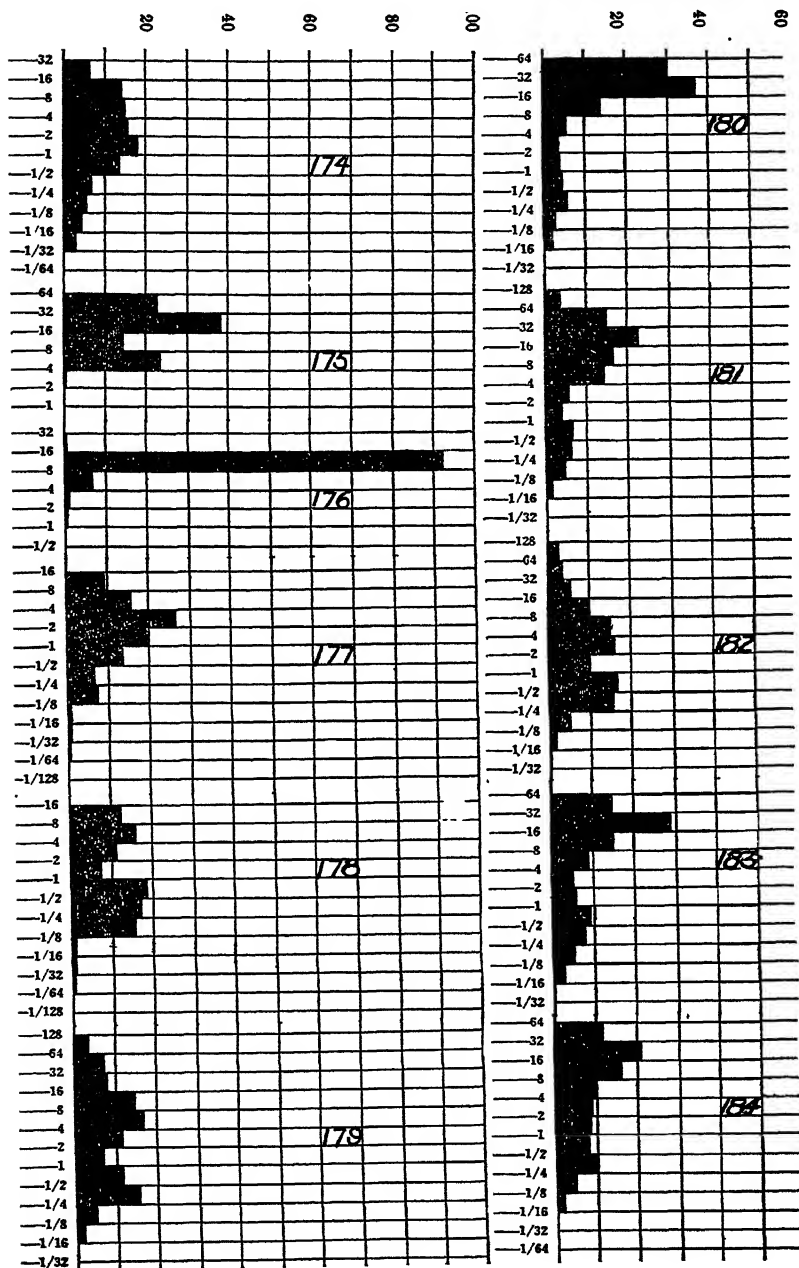
Figure 180 (VIII—146) Creek gravel, Georgia.

Figure 181 (VIII—155) Creek gravel, Georgia.

Figure 182 (VIII—167) Creek gravel, Georgia.

Figure 183 (VIII—224) Creek gravel, Georgia.

Figure 184 (VIII—225) Creek gravel, Georgia.



Figures 174-184

PLATE XIV

FLUVIAL SEDIMENTS

Creek Gravel

Figure 185 (VIII—230) Creek gravel, Georgia.

Figure 186 (II—496) Creek gravel, Maryland.

Figure 187 (II—698) Creek gravel, Pennsylvania.

Creek Sand

Figure 188 (I—59) Creek sand, South Dakota

Figure 189 (I—61) Creek sand, Iowa.

Figure 190 (I—62) Creek sand, Wisconsin.

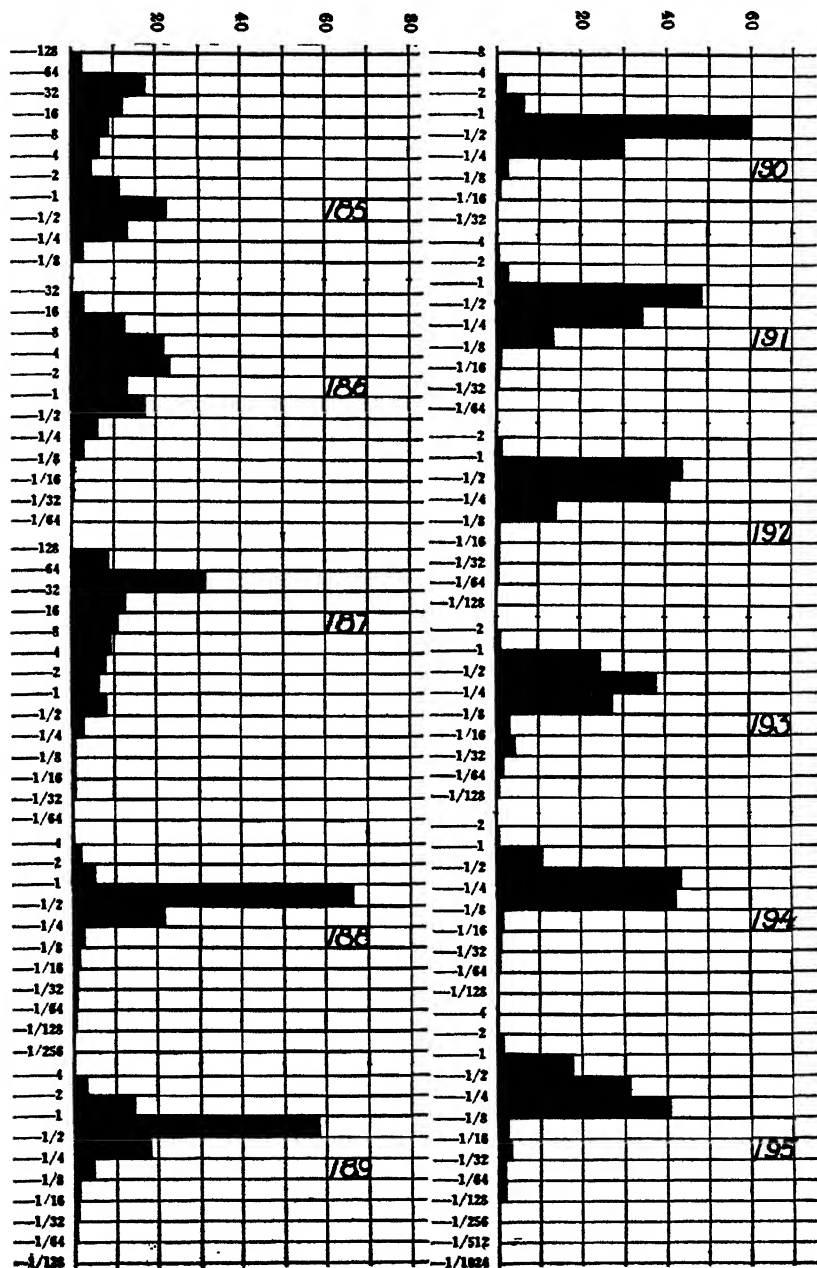
Figure 191 (I—63) Creek sand, Iowa.

Figure 192 (I—64) Creek sand, Iowa.

Figure 193 (I—65) Creek sand, Iowa.

Figure 194 (I—66) Creek sand, Iowa.

Figure 195 (I—67) Creek sand, Iowa



Figures 185-195

PLATE XV

FLUVIAL SEDIMENTS

Creek Sand

Figure 196 (I—68) Creek sand, South Dakota.

Figure 197 (I—69) Creek sand, South Dakota.

Figure 198 (VIII—5) Creek sand, Georgia.

Figure 199 (VIII—93) Creek sand, Georgia.

Figure 200 (VIII—109) Creek sand Georgia.

Figure 201 (VIII—111) Creek sand, Georgia.

Figure 202 (VIII—115) Creek sand, Georgia.

Figure 203 (VIII—126) Creek sand, Georgia.

Figure 204 (VIII—129) Creek sand, Georgia.

Figure 205 (VIII—181) Creek sand, Georgia.

Figure 206 (VIII—222) Creek sand, Georgia.

River Sand

Figure 207 (I—81) River gravel, Iowa.



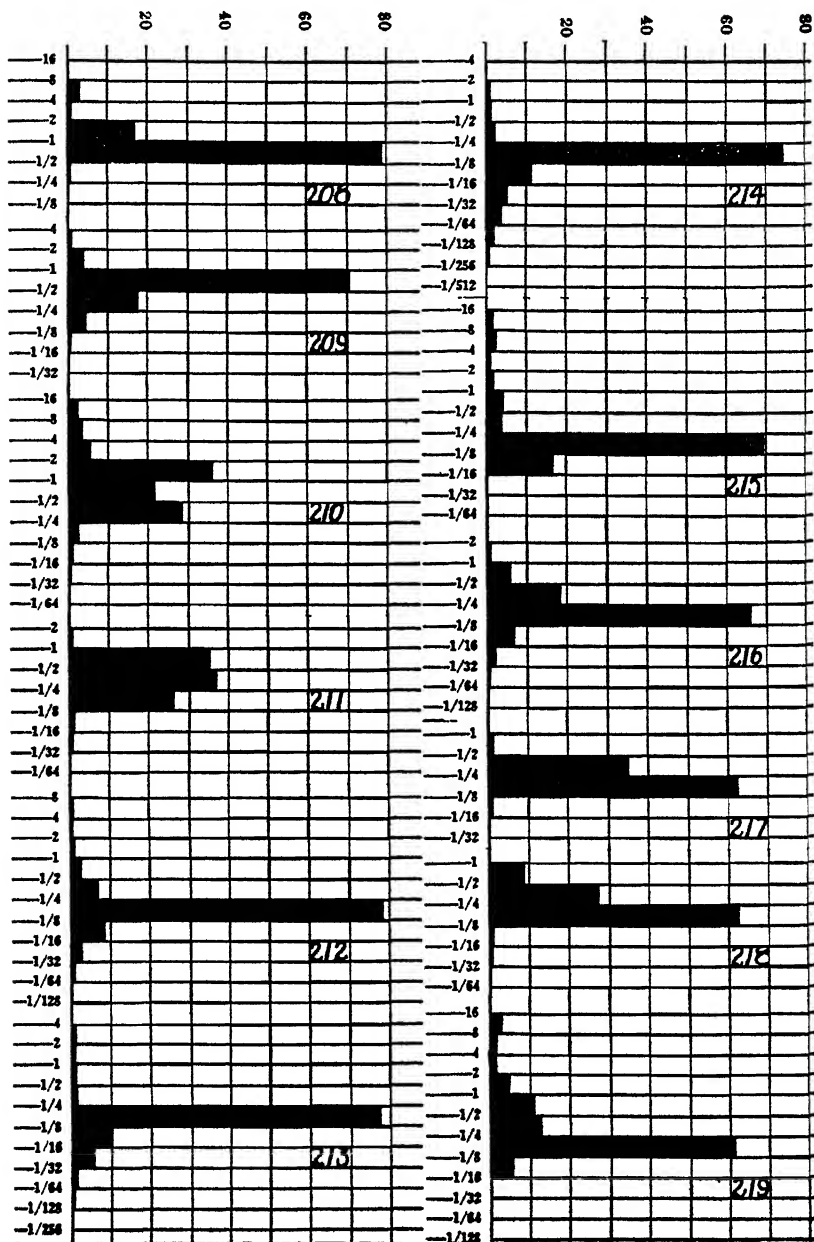
Figures 196-207

PLATE XVI

FLUVIAL SEDIMENTS

River Sand

- Figure 208 (I—82) River sand, Illinois.
Figure 209 (I—83) River sand, Illinois.
Figure 210 (I—84) River sand, Iowa.
Figure 211 (I—85) River sand, Iowa.
Figure 212 (I—86) River sand, Illinois.
Figure 213 (I—87) River sand, Iowa.
Figure 214 (I—88) River sand, from floods, Iowa.
Figure 215 (I—89) River sand, Alaska.
Figure 216 (I—90) River beach sand, Illinois.
Figure 217 (I—91) River beach sand, Iowa.
Figure 218 (I—92) River beach sand, Iowa.
Figure 219 (I—93) River sand, Alaska.



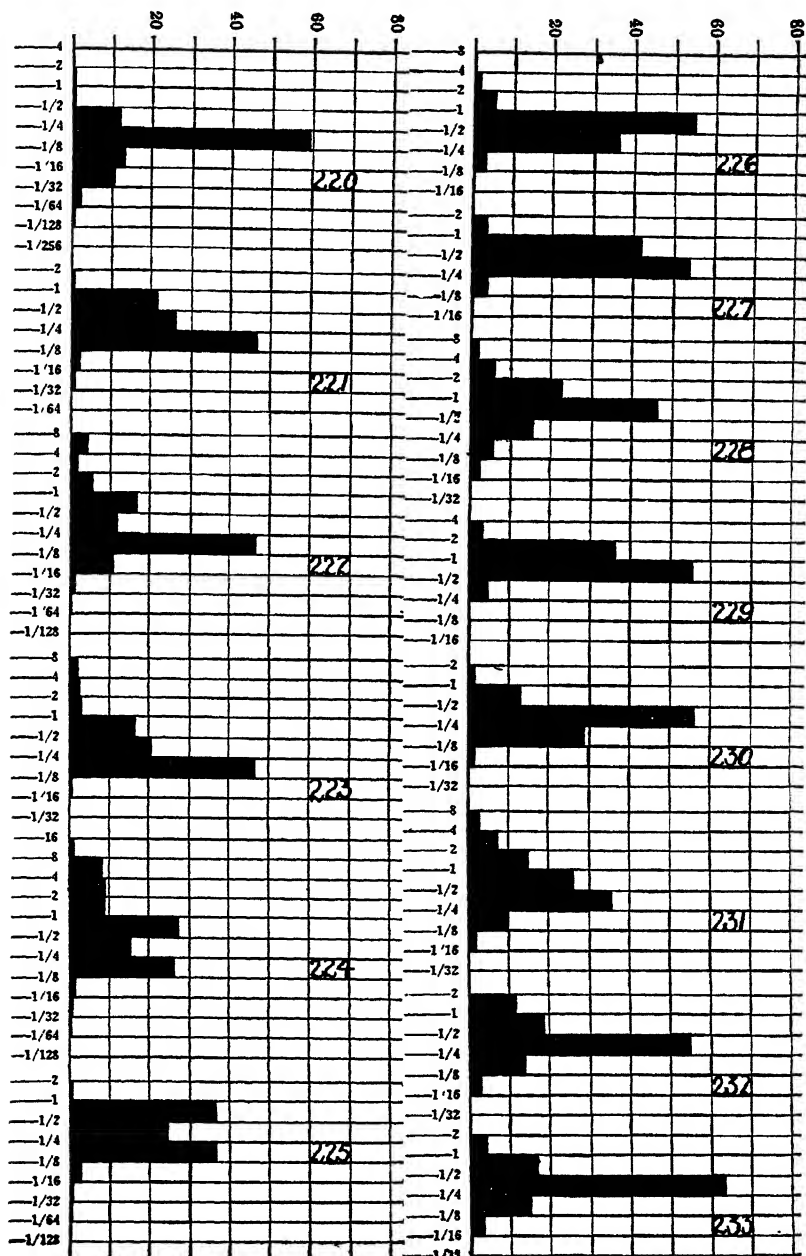
Figures 208-219

PLATE XVII

FLUVIAL SEDIMENTS

River Sand

- Figure 220 (I—94) River sand, Iowa.
Figure 221 (I—95) River bank sand, Iowa.
Figure 222 (I—96) River beach sand, Iowa.
Figure 223 (I—97) River sand, Illinois.
Figure 224 (I—98) River gravel, Iowa.
Figure 225 (I—99) River beach sand, Iowa.
Figure 226 (VIII—13) River sand, Georgia.
Figure 227 (VIII—35) River sand, Georgia.
Figure 228 (VIII—130) River sand, Georgia.
Figure 229 (VIII—207) River sand, Georgia.
Figure 230 (VIII—220) River sand, Georgia.
Figure 231 (VI—154B) River sand, Missouri.
Figure 232 (VI—178) River sand, Missouri.
Figure 233 (VI—180) River sand, Missouri.



Figures 220-233

PLATE XVIII

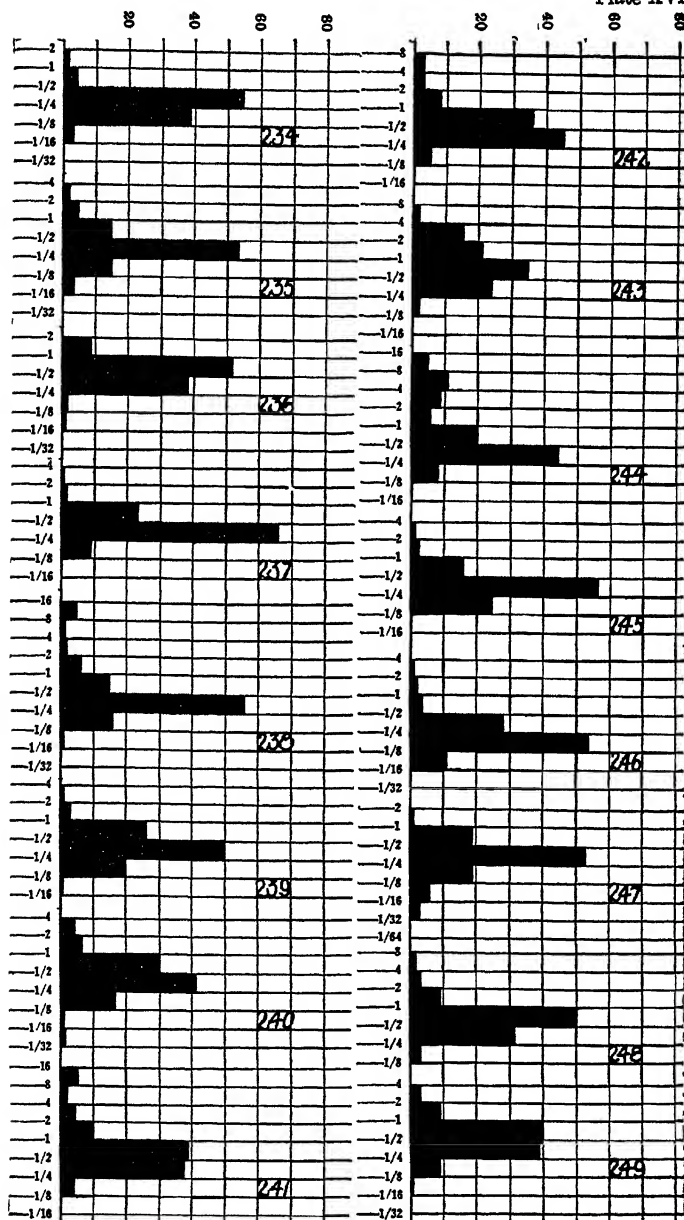
FLUVIAL SEDIMENTS

River Sand

- Figure 234 (VI—193) River sand, Missouri.
Figure 235 (VI—198) Creek sand, Missouri.
Figure 236 (XI—1729A) River sand, Virginia.

Channel Sand

- Figure 237 (XII— 4) Mississippi River.
Figure 238 (XII— 9) Mississippi River.
Figure 239 (XII— 10) Mississippi River.
Figure 240 (XII— 15) Mississippi River.
Figure 241 (XII— 16) Mississippi River.
Figure 242 (XII— 17) Mississippi River.
Figure 243 (XII— 18) Mississippi River.
Figure 244 (XII— 19) Mississippi River.
Figure 245 (XII— 20) Mississippi River.
Figure 246 (XII— 21) Mississippi River.
Figure 247 (XII— 22) Mississippi River.
Figure 248 (XII— 26) Mississippi River.
Figure 249 (XII— 27) Mississippi River.



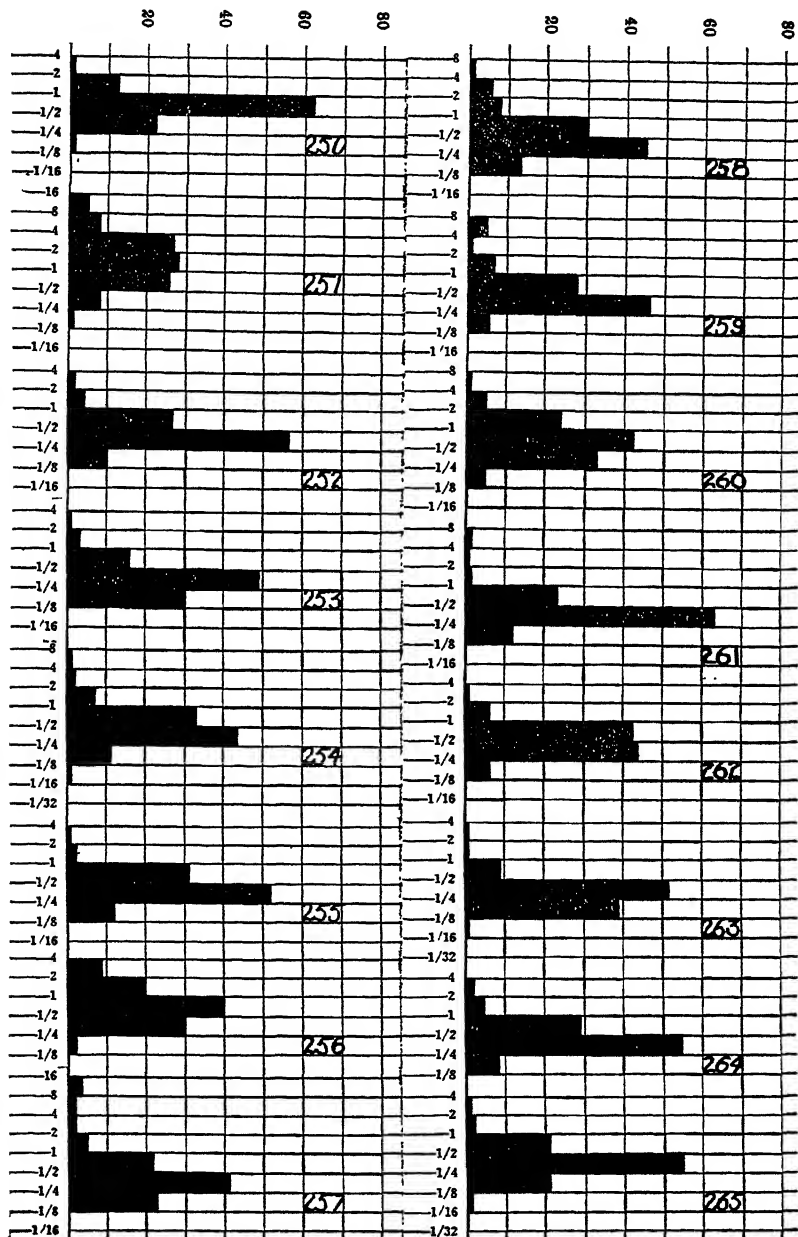
Figures 234-249

PLATE XIX

FLUVIAL SEDIMENTS

Channel Sand

- Figure 250 (XII— 36) Mississippi River.
Figure 251 (XII— 51) Mississippi River.
Figure 252 (XII— 52) Mississippi River.
Figure 253 (XII— 53) Mississippi River.
Figure 254 (XII— 54) Mississippi River.
Figure 255 (XII— 55) Mississippi River.
Figure 256 (XII— 56) Mississippi River.
Figure 257 (XII— 57) Mississippi River.
Figure 258 (XII— 58) Mississippi River.
Figure 259 (XII— 59) Mississippi River.
Figure 260 (XII— 65) Mississippi River.
Figure 261 (XII— 67) Mississippi River.
Figure 262 (XII— 68) Mississippi River.
Figure 263 (XII— 69) Mississippi River.
Figure 264 (XII— 74) Mississippi River.
Figure 265 (XII— 78) Mississippi River.



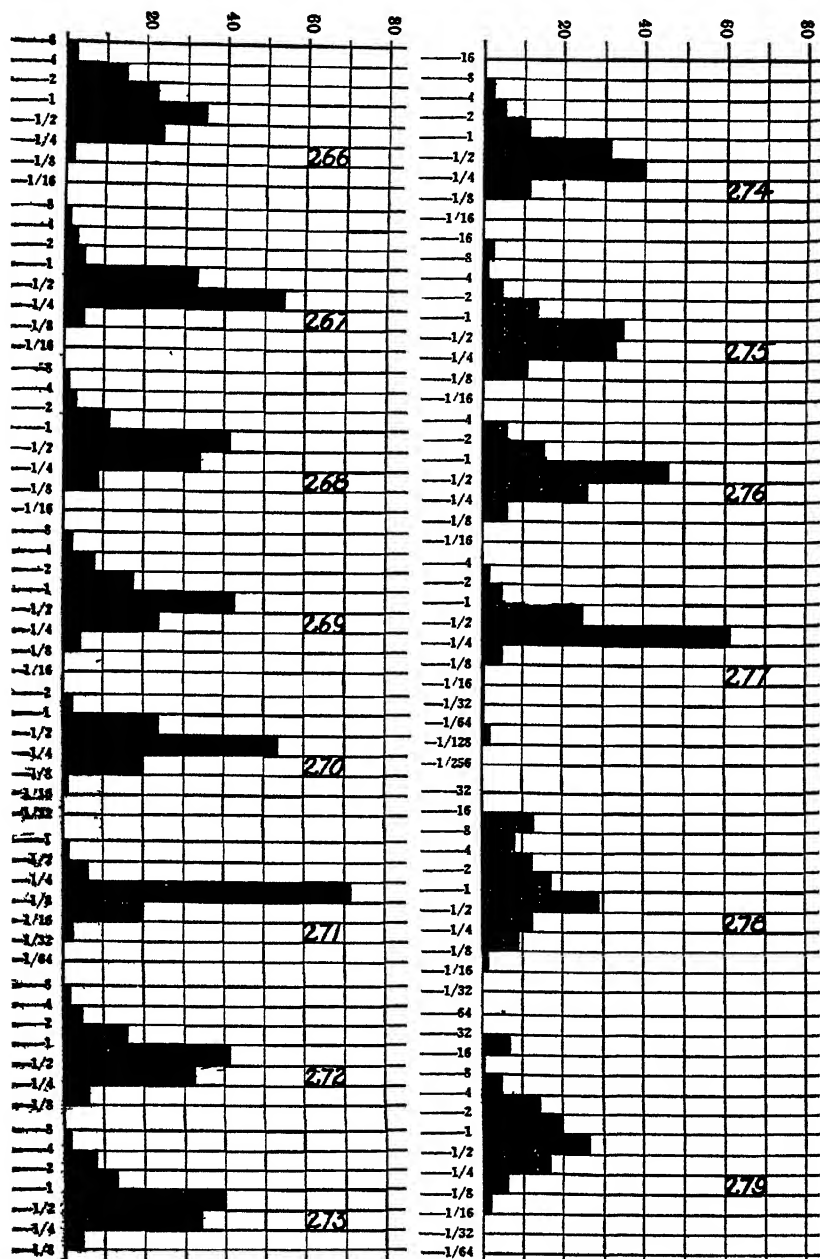
Figures 250-265

PLATE XX

FLUVIAL SEDIMENTS

Channel Sand

- Figure 266 (XII— 79) Mississippi River.
- Figure 267 (XII— 81) Mississippi River.
- Figure 268 (XII— 90) Mississippi River.
- Figure 269 (XII— 91) Mississippi River.
- Figure 270 (XII— 92) Mississippi River.
- Figure 271 (XII— 93) Mississippi River.
- Figure 272 (XII— 94) Mississippi River.
- Figure 273 (XII—100) Mississippi River.
- Figure 274 (XII—109) Mississippi River.
- Figure 275 (XII—114) Mississippi River.
- Figure 276 (XII—117) Mississippi River.
- Figure 277 (XII—120) Mississippi River.
- Figure 278 (XII—138) Mississippi River.
- Figure 279 (XII—143) Mississippi River.



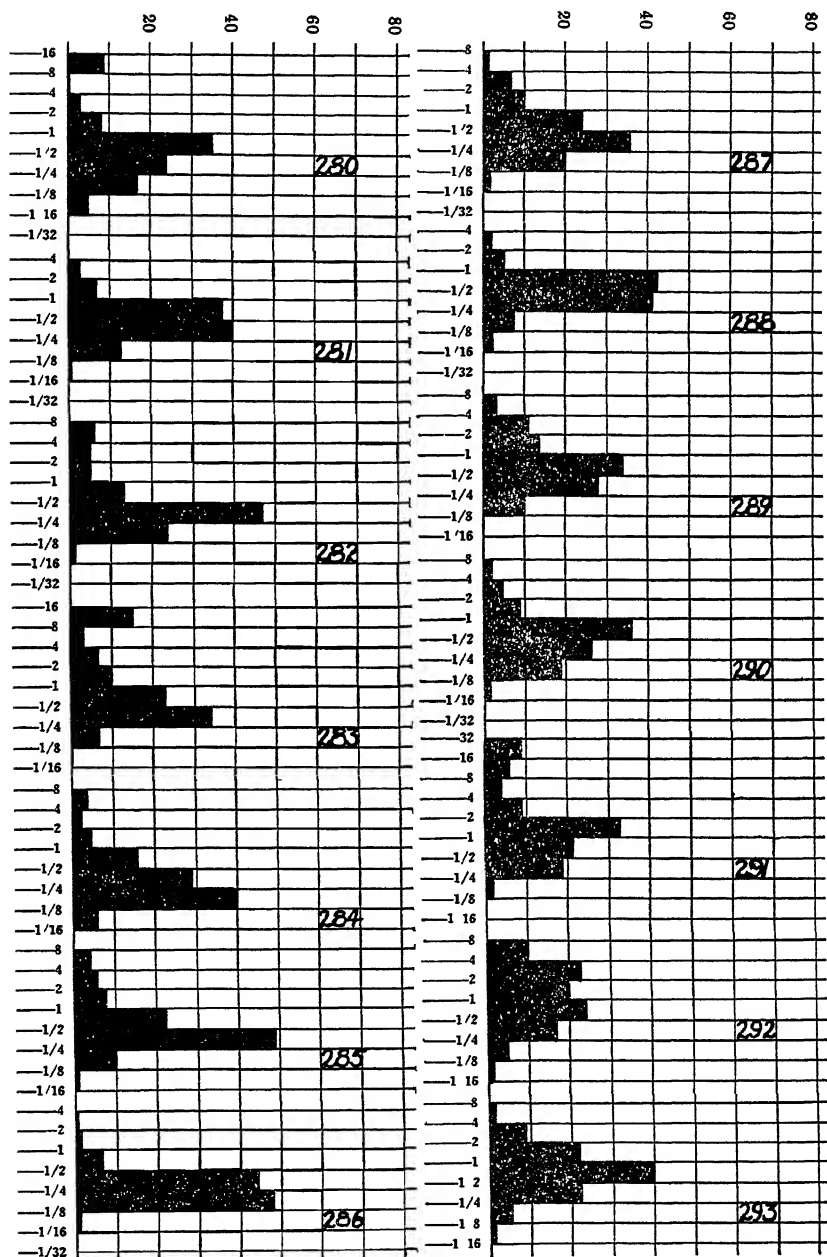
Figures 266-279

PLATE XXI

FLUVIAL SEDIMENTS

Channel Sand

- Figure 280 (XII—144) Mississippi River.
Figure 281 (XII—147) Mississippi River.
Figure 282 (XII—148) Mississippi River.
Figure 283 (XII—149) Mississippi River.
Figure 284 (XII—153) Mississippi River.
Figure 285 (XII—155) Mississippi River.
Figure 286 (XII—163) Mississippi River.
Figure 287 (XII—172) Mississippi River.
Figure 288 (XII—173) Mississippi River.
Figure 289 (XII—185) Mississippi River.
Figure 290 (XII—186) Mississippi River.
Figure 291 (XII—187) Mississippi River.
Figure 292 (XII—189) Mississippi River.
Figure 293 (XII—196) Mississippi River.



Figures 280-293

PLATE XXII

FLUVIAL SEDIMENTS

Channel Sand

Figure 294 (XII—197) Mississippi River.

Figure 295 (XII—198) Mississippi River.

Figure 296 (XII—199) Mississippi River.

Figure 297 (XII—200) Mississippi River.

Figure 298 (XII—207) Mississippi River.

Figure 299 (XII—208) Mississippi River.

Figure 300 (XII—216) Mississippi River.

Figure 301 (XII—217) Mississippi River.

Figure 302 (XII—221) Mississippi River.

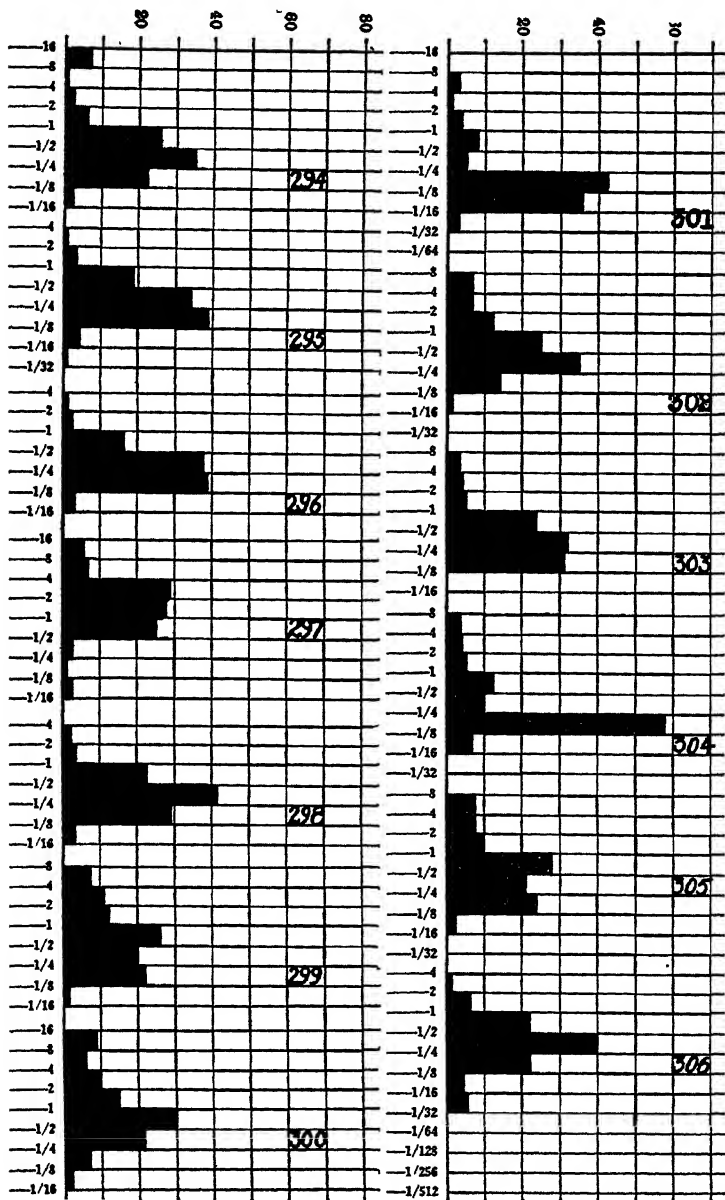
Figure 303 (XII—224) Mississippi River.

Figure 304 (XII—225) Mississippi River.

Figure 305 (XII—235) Mississippi River.

Sediments from Positions Slightly Off Channels

Figure 306 (XII— 6) Mississippi River.



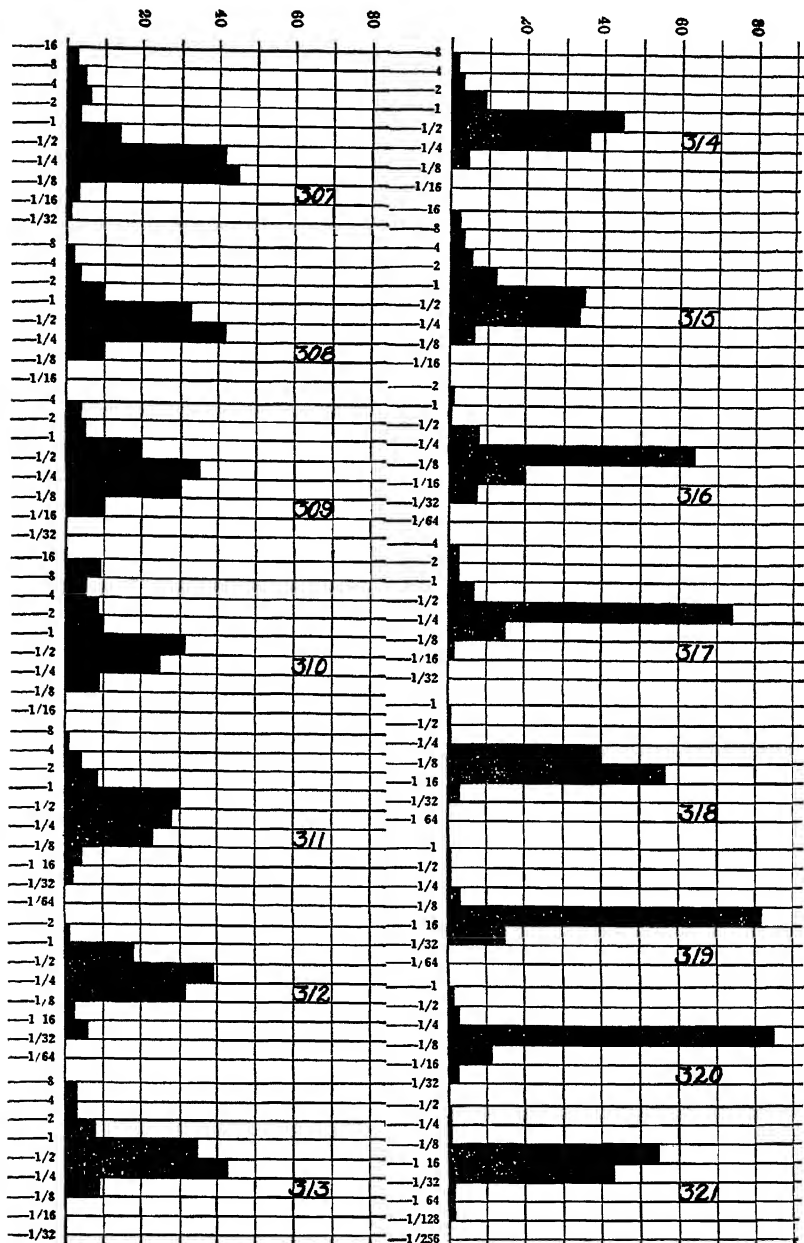
Figures 294-306

PLATE XXIII

FLUVIAL SEDIMENTS

Sediments from Positions Slightly Off Channels

- Figure 307 (XII— 11) Mississippi River.
- Figure 308 (XII— 23) Mississippi River.
- Figure 309 (XII— 24) Mississippi River.
- Figure 310 (XII— 25) Mississippi River.
- Figure 311 (XII— 47) Mississippi River.
- Figure 312 (XII— 71) Mississippi River.
- Figure 313 (XII— 75) Mississippi River.
- Figure 314 (XII— 76) Mississippi River.
- Figure 315 (XII— 77) Mississippi River.
- Figure 316 (XII—137) Mississippi River.
- Figure 317 (XII—142) Mississippi River.
- Figure 318 (XII—145) Mississippi River.
- Figure 319 (XII—151) Mississippi River.
- Figure 320 (XII—152) Mississippi River.
- Figure 321 (XII—156) Mississippi River.



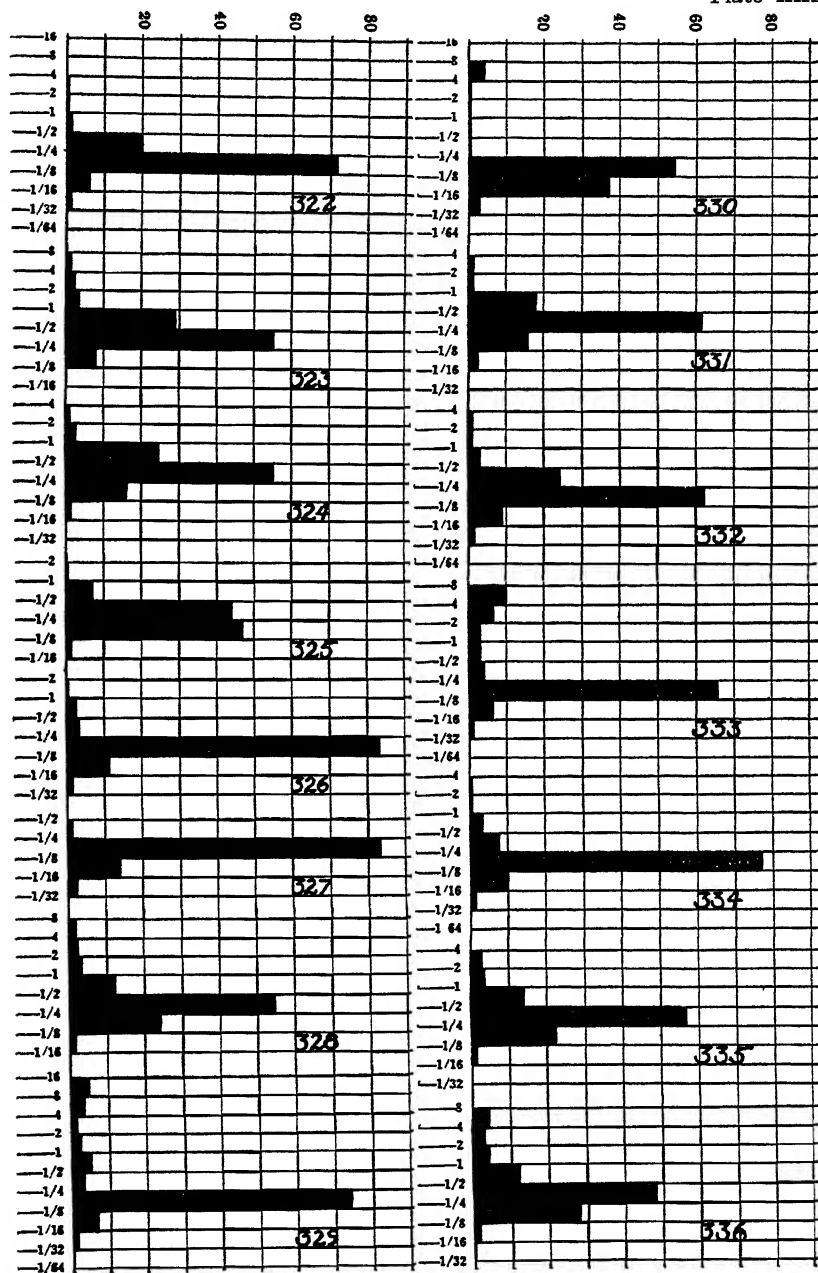
Figures 307-321

PLATE XXIV

FLUVIAL SEDIMENTS

Sediments from Positions Slightly Off Channels

- Figure 322 (XII—158) Mississippi River.
- Figure 323 (XII—162) Mississippi River.
- Figure 324 (XII—164) Mississippi River.
- Figure 325 (XII—171) Mississippi River.
- Figure 326 (XII—175) Mississippi River.
- Figure 327 (XII—177) Mississippi River.
- Figure 328 (XII—188) Mississippi River.
- Figure 329 (XII—190) Mississippi River.
- Figure 330 (XII—191) Mississippi River.
- Figure 331 (XII—202) Mississippi River.
- Figure 332 (XII—204) Mississippi River.
- Figure 333 (XII—209) Mississippi River.
- Figure 334 (XII—212) Mississippi River.
- Figure 335 (XII—222) Mississippi River.
- Figure 336 (XII—223) Mississippi River.



Figures 322-336

PLATE XXV

FLUVIAL SEDIMENTS

Sediments from Positions Slightly Off Channels

Figure 337 (XII—226) Mississippi River.

Figure 338 (XII—227) Mississippi River.

Figure 339 (XII—234) Mississippi River.

Slack Water Sediments, Considerably Away from Main
Channels

Figure 340 (XII— 33) Mississippi River.

Figure 341 (XII— 82) Mississippi River.

Figure 342 (XII— 83) Mississippi River.

Figure 343 (XII— 85) Mississippi River.

Figure 344 (XII— 86) Mississippi River.

Figure 345 (XII— 87) Mississippi River.

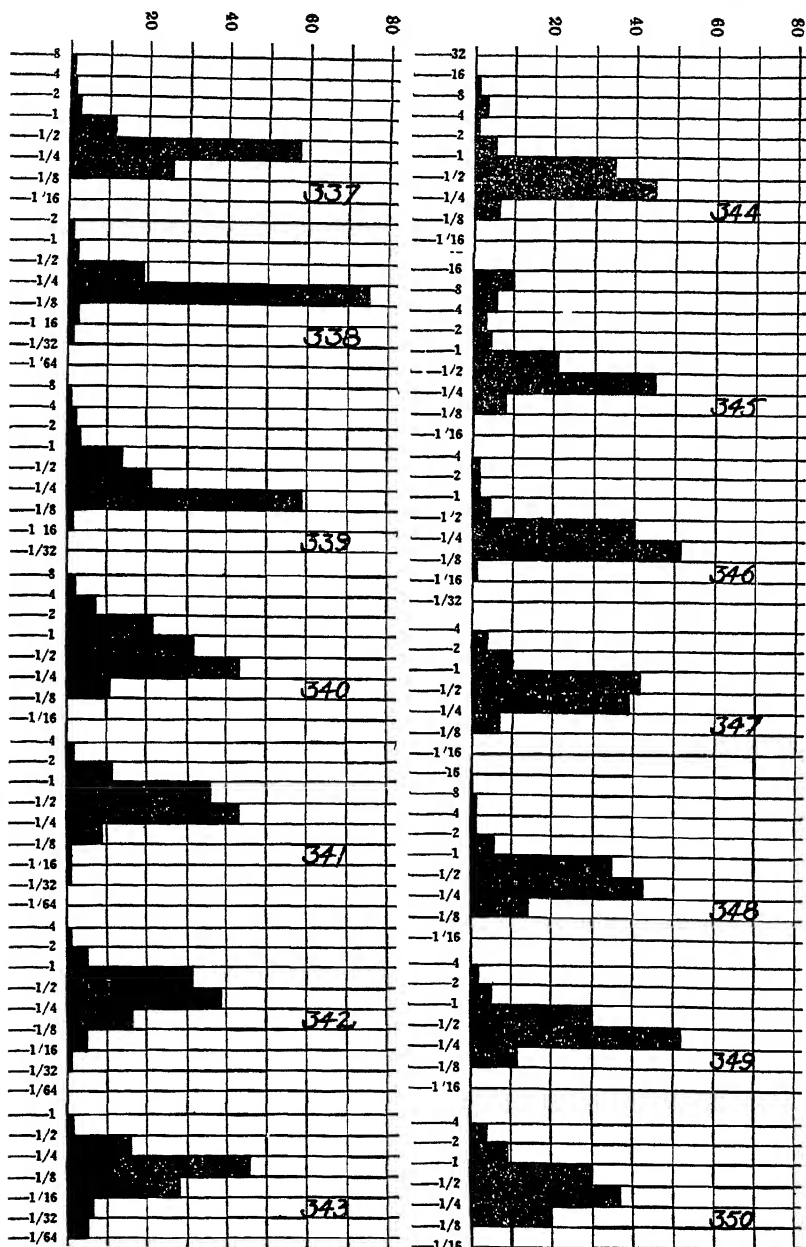
Figure 346 (XII— 88) Mississippi River.

Figure 347 (XII— 95) Mississippi River.

Figure 348 (XII— 96) Mississippi River.

Figure 349 (XII— 97) Mississippi River.

Figure 350 (XII— 98) Mississippi River.



Figures 337-350

PLATE XXVI

FLUVIAL SEDIMENTS

Slack Water Sediments, Considerably Away from Main
Channels

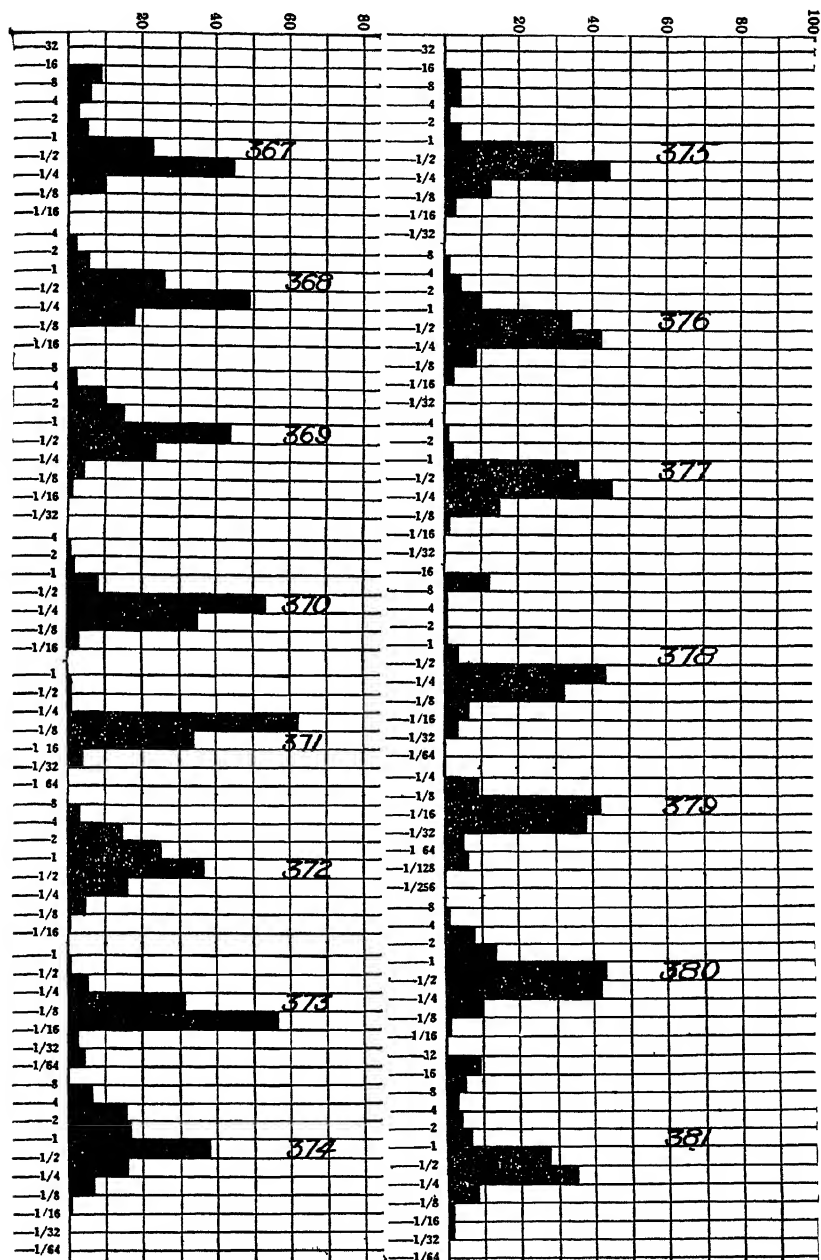
- Figure 351 (XII—101) Mississippi River.
- Figure 352 (XII—102) Mississippi River.
- Figure 353 (XII—103) Mississippi River.
- Figure 354 (XII—104) Mississippi River.
- Figure 355 (XII—106) Mississippi River.
- Figure 356 (XII—107) Mississippi River.
- Figure 357 (XII—108) Mississippi River.
- Figure 358 (XII—110) Mississippi River.
- Figure 359 (XII—112) Mississippi River.
- Figure 360 (XII—115) Mississippi River.
- Figure 361 (XII—116) Mississippi River.
- Figure 362 (XII—122) Mississippi River.
- Figure 363 (XII—123) Mississippi River.
- Figure 364 (XII—124) Mississippi River.
- Figure 365 (XII—126) Mississippi River.
- Figure 366 (XII—127) Mississippi River.

PLATE XXVII

FLUVIAL SEDIMENTS

Slack Water Sediments, Considerably Away from Main
Channels

- Figure 367 (XII—128) Mississippi River.
- Figure 368 (XII—131) Mississippi River.
- Figure 369 (XII—139) Mississippi River.
- Figure 370 (XII—140) Mississippi River.
- Figure 371 (XII—141) Mississippi River.
- Figure 372 (XII—174) Mississippi River.
- Figure 373 (XII—176) Mississippi River.
- Figure 374 (XII—178) Mississippi River.
- Figure 375 (XII—201) Mississippi River.
- Figure 376 (XII—203) Mississippi River.
- Figure 377 (XII—211) Mississippi River.
- Figure 378 (XII—213) Mississippi River.
- Figure 379 (XII—214) Mississippi River.
- Figure 380 (XII—215) Mississippi River.
- Figure 381 (XII—231) Mississippi River.



Figures 367-381

PLATE XXVIII

FLUVIAL SEDIMENTS

Slack Water Sediments, Considerably Away from Main
Channels

Figure 382 (XII—232) Mississippi River.

Figure 383 (XII—233) Mississippi River.
River Bar Sand

Figure 384 (XII— 3) Mississippi River.

Figure 385 (XII— 5) Mississippi River.

Figure 386 (XII—154) Mississippi River.

Figure 387 (XII—160) Mississippi River.

Figure 388 (XII—167) Mississippi River.

Figure 389 (XII—168) Mississippi River.

Figure 390 (XII—169) Mississippi River.

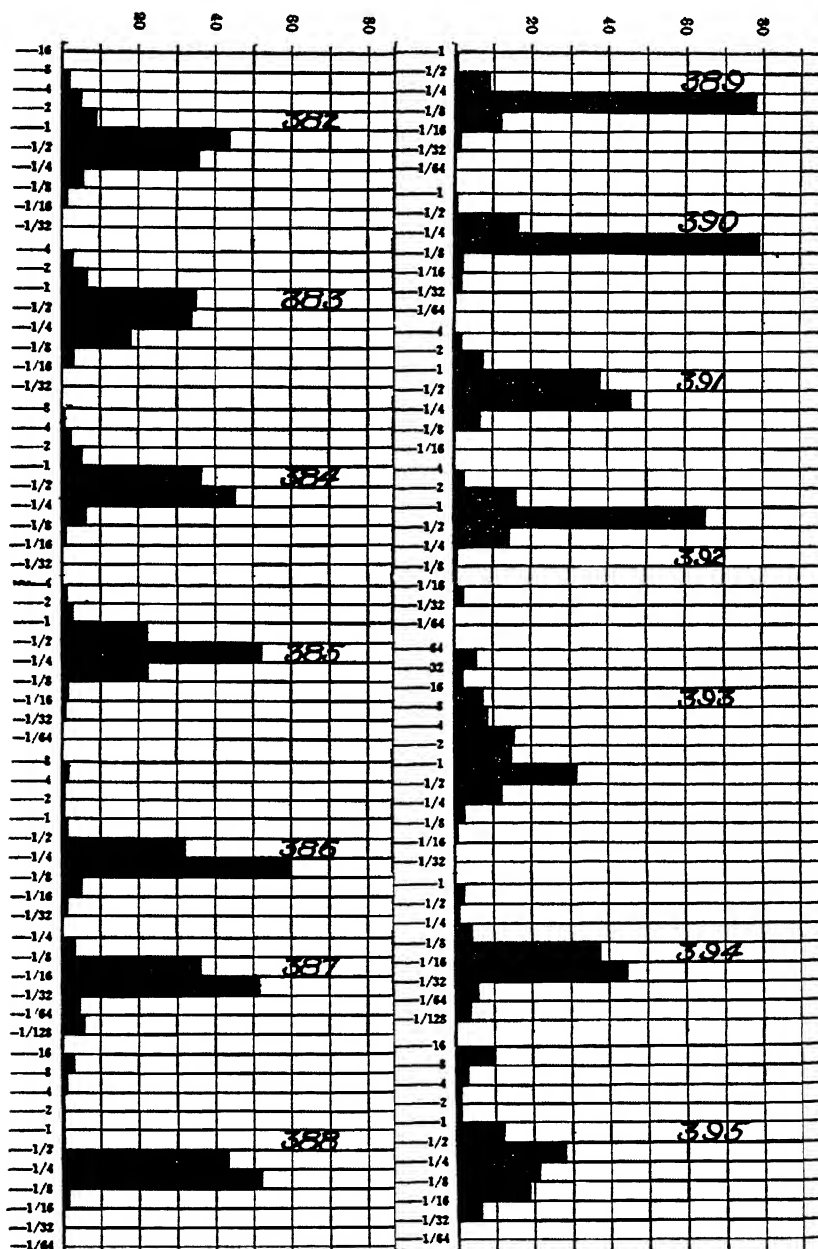
Figure 391 (XII—170) Mississippi River.

Figure 392 (XII—180) Mississippi River.

Figure 393 (XII—181) Mississippi River.

Figure 394 (XII—183) Mississippi River.

Figure 395 (XII—218) Mississippi River.



Figures 382-395

PLATE XXIX

FLUVIAL SEDIMENTS

River Bar Sand

Figure 396 (XII—229) Mississippi River.

Figure 397 (XI—1729B) River bar sand, Virginia.

Figure 398 (XI—1729C) River bar sand and pebbles, Virginia.

Figure 399 (VIII—110) River bar sand, Georgia.

Figure 400 (VIII—214) River bar sand, Georgia.

Figure 401 (VIII—241) River bar sand, Georgia.

Figure 402 (VI—211) River bar sand, Missouri.

River Lag Sand and Gravel

Figure 403 (XI—1729D) River lag sand, Virginia.

Figure 404 (XII— 46) Lag gravel, Mississippi River.

Figure 405 (XII— 60) Lag gravel, Mississippi River.

Figure 406 (XII—132) Lag gravel, Mississippi River.

Figure 407 (XII—179) Lag gravel, Mississippi River.

Figure 408 (XII—193) Lag gravel, Mississippi River.

Figure 409 (XII—194) Lag sand, Mississippi River.

MECHANICAL COMPOSITION OF SEDIMENTS 67

Plate XXIX

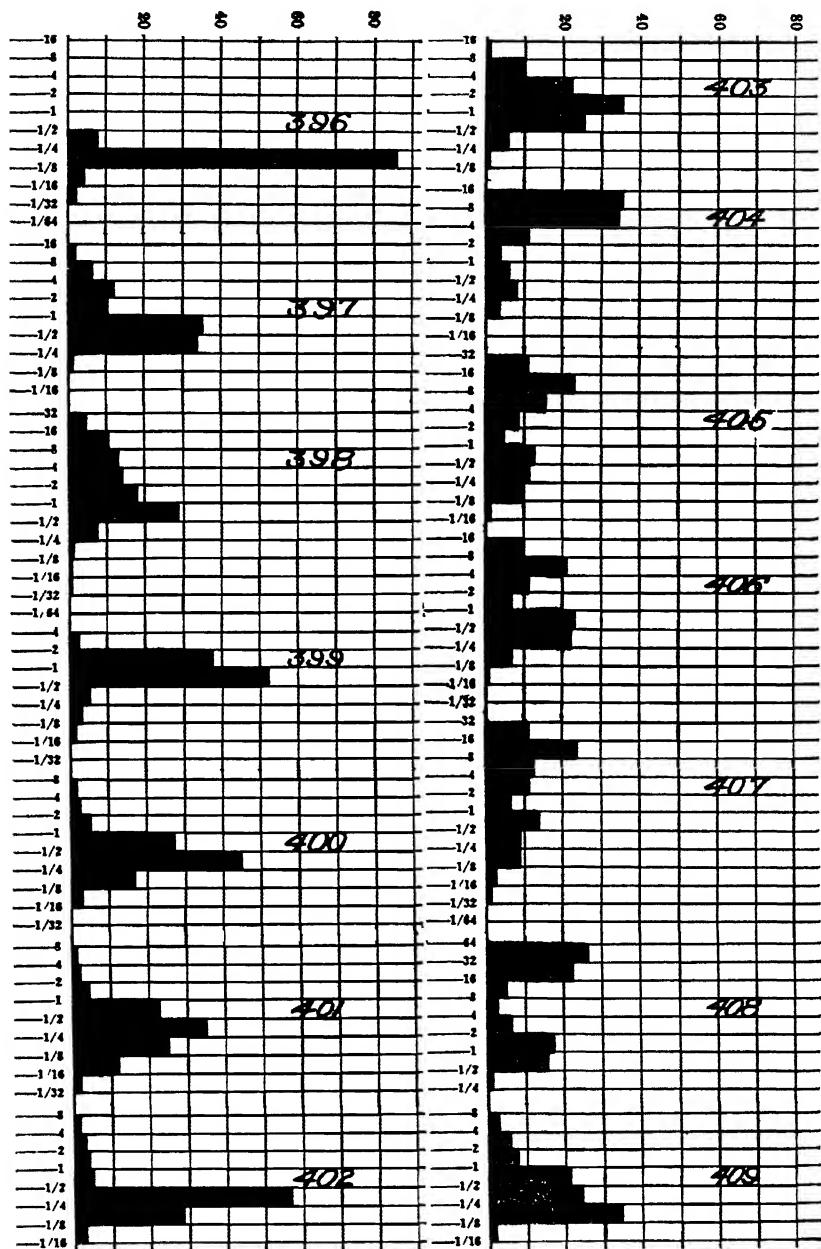
**Figures 396-409**

PLATE XXX

FLUVIAL SEDIMENTS

River Lag Sand and Gravel

Figure 410 (XII—220) Lag sand, Mississippi River.

Sand from Small Dry Channels

Figure 411 (III— 81) Medium sand from dry channel, Island of Oahu.

Figure 412 (III—664B) Medium sand from dry channel, Island of Oahu.

Figure 413 (III— 841) Medium sand from dry channel, Island of Oahu.

Figure 414 (III—1821) Medium sand from dry channel, Island of Oahu.

Figure 415 (III—1859) Medium sand from dry channel, Island of Oahu.

Figure 416 (III—1860) Medium sand from dry channel, Island of Oahu.

Fluvial Terrace Materials

Figure 417 (I—24) Terrace gravel, Illinois.

Figure 418 (I—25) Terrace gravel, Illinois.

Figure 419 (I—26) Terrace gravel, Illinois.

Figure 420 (I—27) Terrace gravel, Illinois.

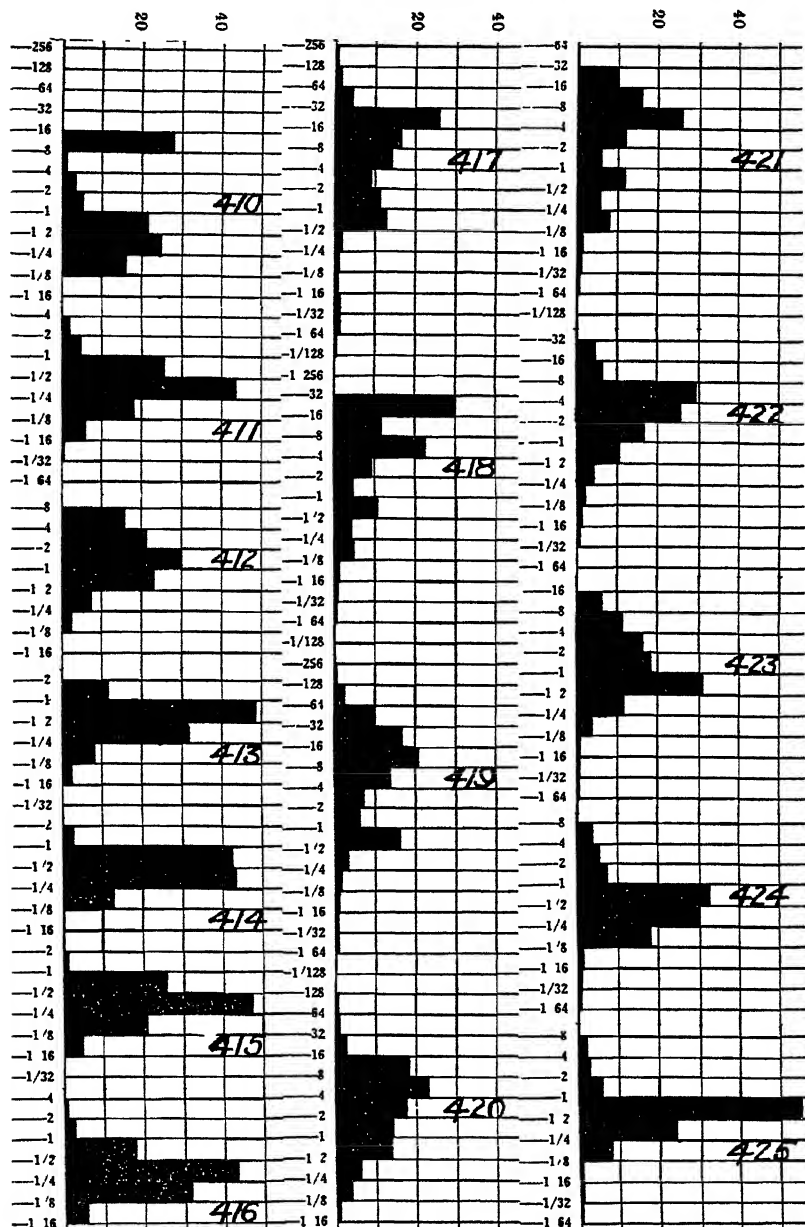
Figure 421 (I—28) Terrace gravel, Illinois.

Figure 422 (I—29) Terrace gravel, Illinois.

Figure 423 (I—30) Terrace gravel, Illinois.

Figure 424 (I—31) Terrace sand, Illinois.

Figure 425 (I—32) Terrace sand, Illinois.



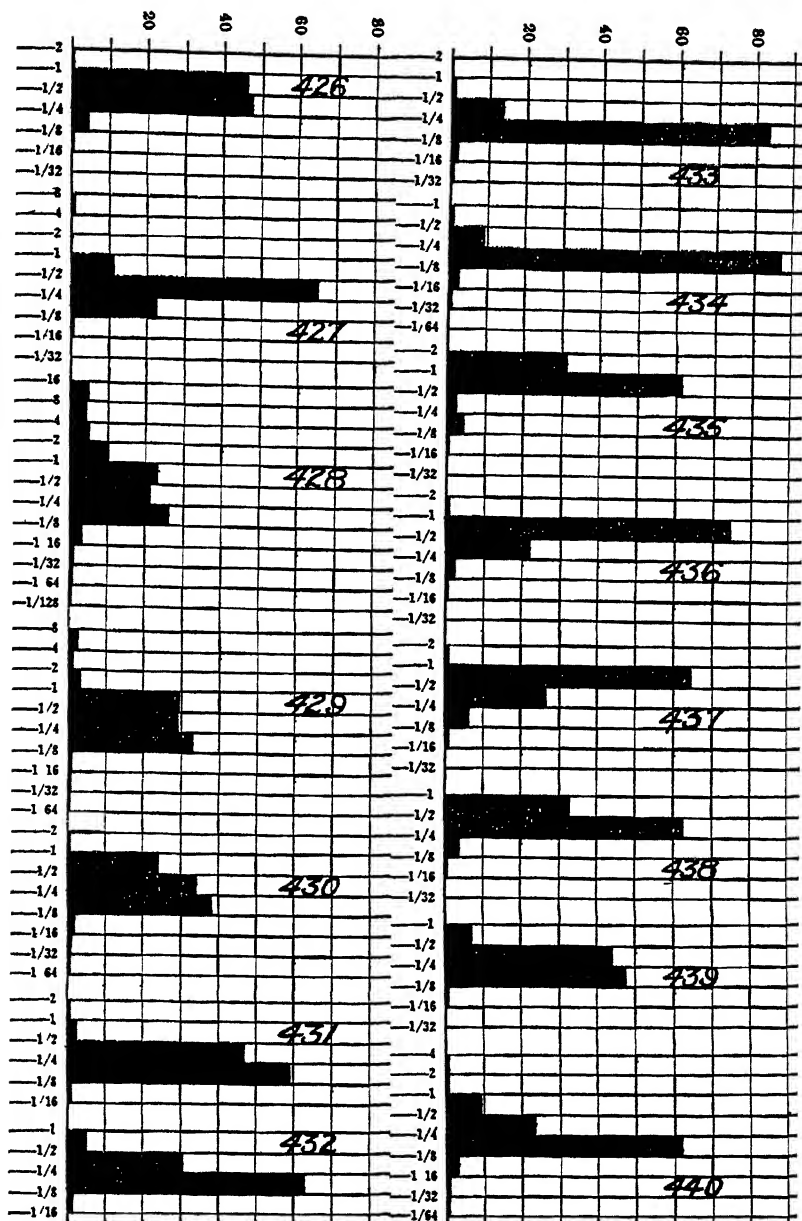
Figures 410-425

PLATE XXXI

FLUVIAL SEDIMENTS

Fluvial Terrace Materials

- Figure 426 (I—33) Terrace sand, cross-bedded, Illinois.
Figure 427 (I—34) Sand from single oblique layer, Illinois.
Figure 428 (I—35) Terrace gravel, Illinois.
Figure 429 (I—36) Terrace sand, Illinois.
Terrace Materials, Single Layers
Figure 430 (I—19) Glacial sand, Illinois.
Figure 431 (I—20) Glacial sand, Illinois.
Figure 432 (I—21) Glacial sand, from single oblique layer,
Illinois.
Figure 433 (I—22) Glacial sand, Illinois.
Figure 434 (I—23) Glacial sand, Illinois.
Figure 435 (I—37) Terrace sand, Illinois.
Figure 436 (I—39) Terrace sand, Illinois.
Figure 437 (I—40) Sand from oblique layer, Illinois.
Figure 438 (I—41) Sand from oblique layer, Illinois.
Figure 439 (I—42) Sand from oblique layer, Illinois.
Figure 440 (I—43) Terrace sand, Iowa.



Figures 426-440

PLATE XXXII

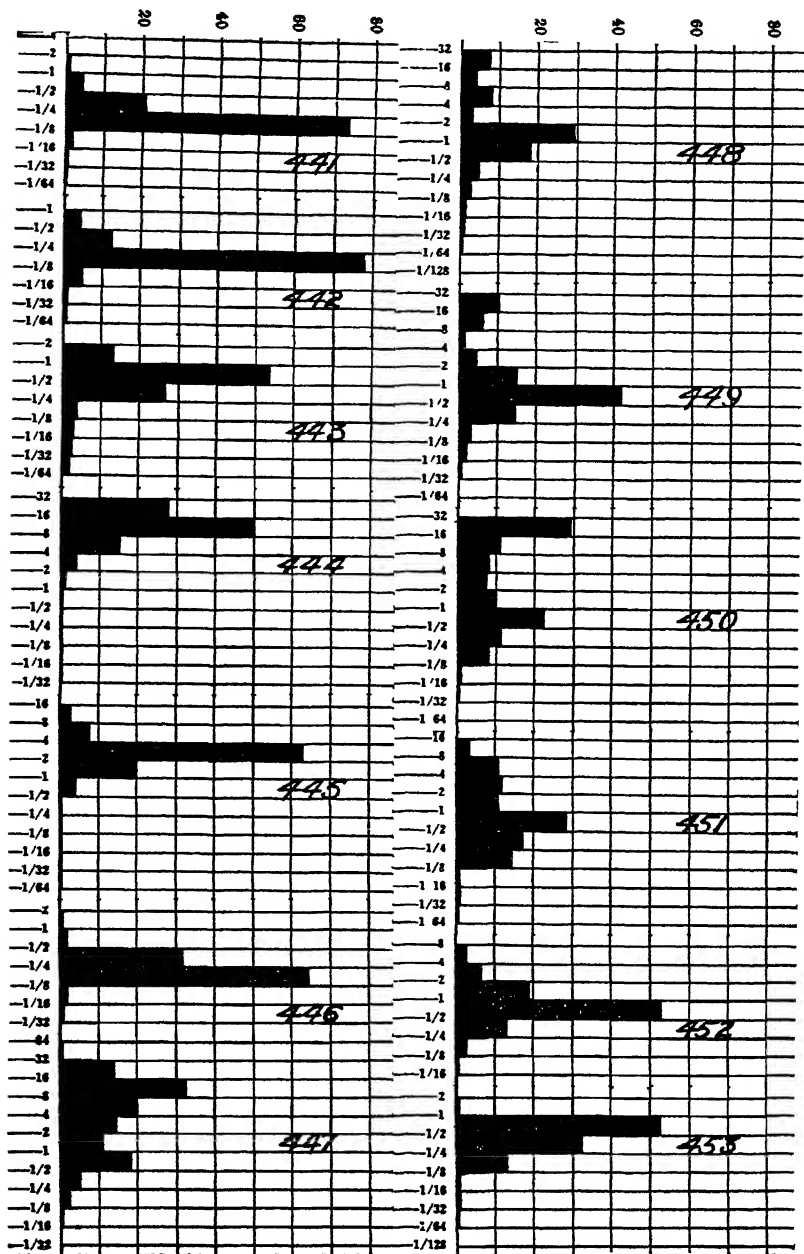
FLUVIAL SEDIMENTS

Terrace Materials, Single Layers

- Figure 441 (I—44) Sand from oblique layer, Illinois.
Figure 442 (I—45) Sand from single layer, Illinois.
Figure 443 (VI—175) Glacial sand, Missouri.
Figure 444 (II—334A) Terrace gravel from single layer,
Maryland.
Figure 445 (II—334D) Terrace gravel from single layer,
Maryland.
Figure 446 (II—334E) Terrace sand from single layer, Mary-
land.

Fluvio-glacial Sediments

- Figure 447 (I— 9) Glacial terrace gravel, Illinois.
Figure 448 (I—10) Glacial gravel from pocket in till, Illinois.
Figure 449 (I—11) Glacial terrace gravel, Illinois.
Figure 450 (I—12) Glacial terrace gravel, Illinois.
Figure 451 (I—13) Glacial gravel, South Dakota.
Figure 452 (I—14) Glacial terrace gravel, Illinois.
Figure 453 (I—15) Glacial sand, Iowa.



Figures 441-453

PLATE XXXIII

FLUVIAL SEDIMENTS

Fluvio-glacial Sediments

Figure 454 (I—16) Glacial terrace sand, Illinois

Figure 455 (I—17) Glacial terrace sand, Illinois.

Figure 456 (I—18) Glacial terrace sand, Illinois.

Silt from Large Streams

Figure 457 (I—100) Alluvium, Iowa.

Figure 458 (I—101) Alluvium, Iowa.

Figure 459 (I—102) Alluvium, Iowa.

Figure 460 (I—103) Alluvium, Illinois.

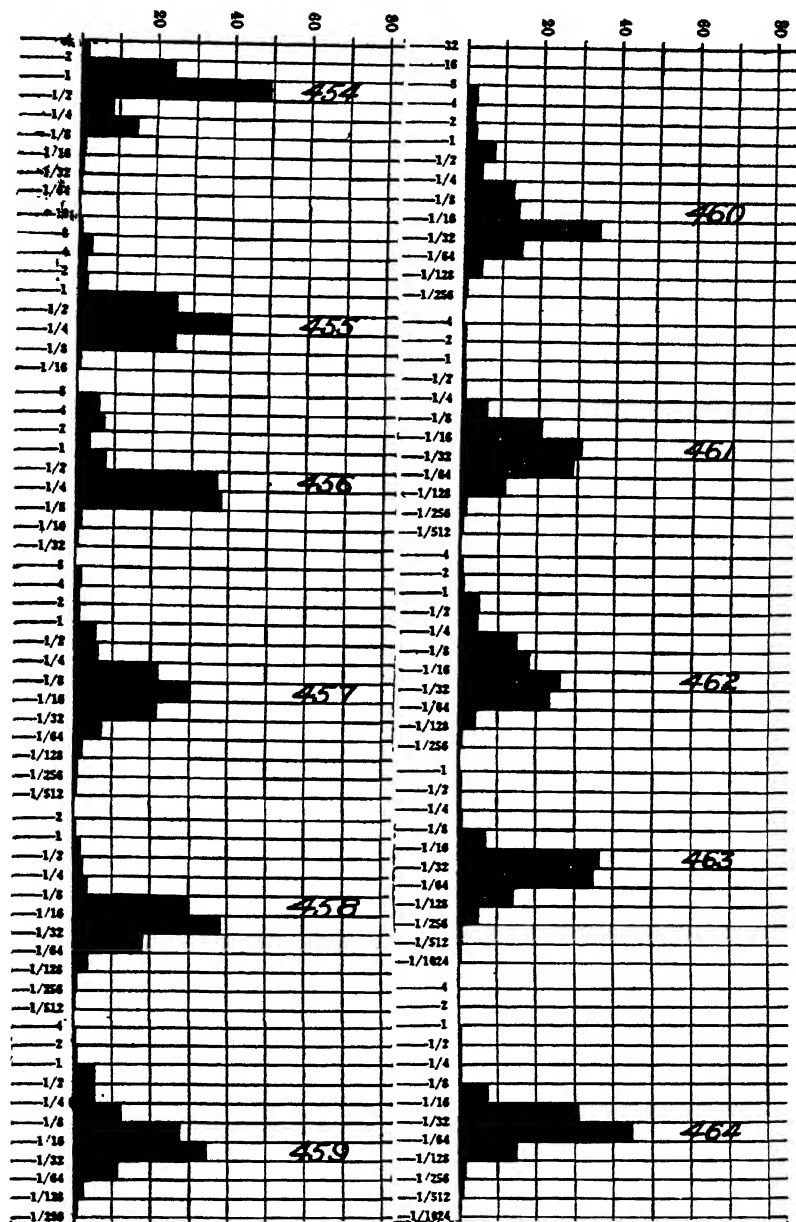
Figure 461 (I—104) Alluvium, Iowa.

Silt from Mississippi Terraces

Figure 462 (I—37) Terrace material, Iowa.

Figure 463 (I—46) Glacial silt, single layer, Iowa.

Figure 464 (I—47) Glacial silt, single layer, Iowa.



Figures 454-464

PLATE XXXIV

FLUVIAL SEDIMENTS

Silt from Mississippi Terraces

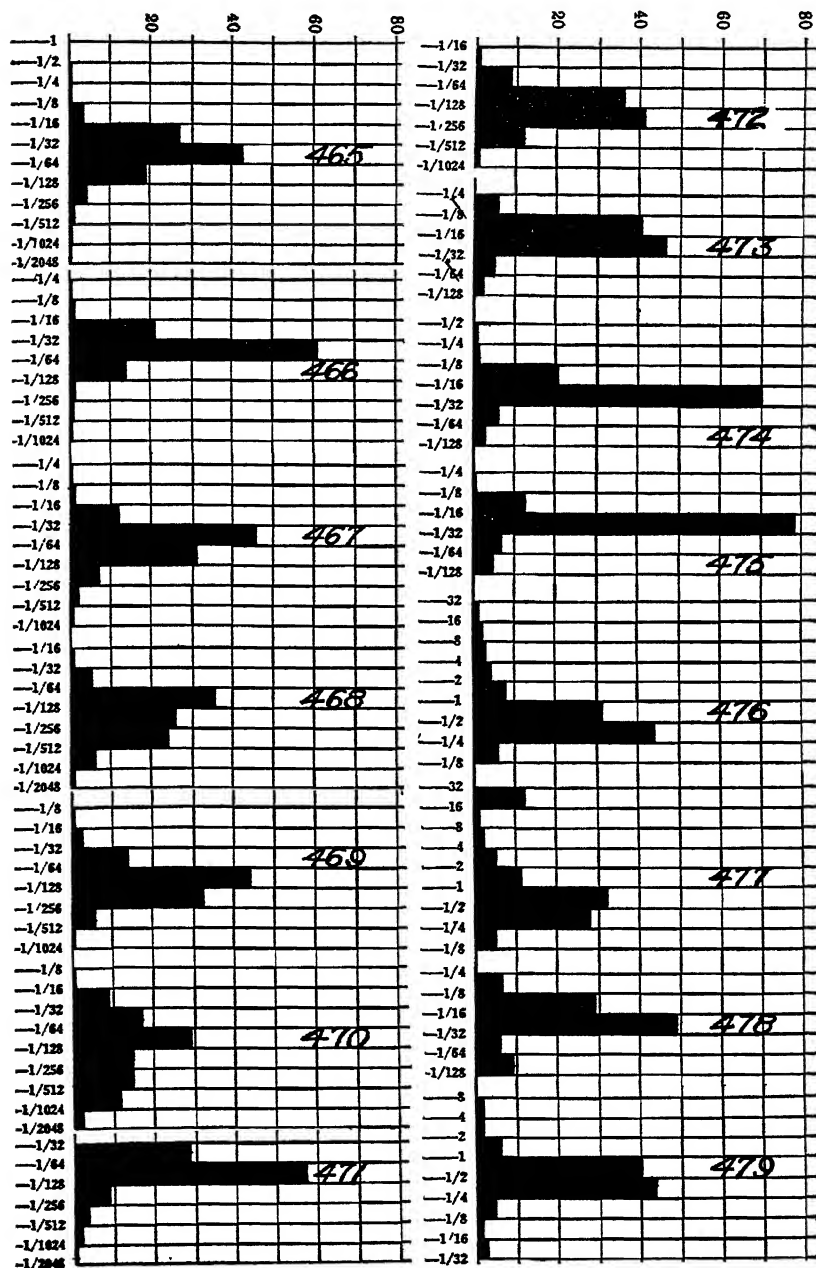
- Figure 465 (I—48) Glacial silt, Iowa.
- Figure 466 (I—49) Glacial silt, single layer, Iowa.
- Figure 467 (I—50) Glacial silt, single layer, Iowa.
- Figure 468 (I—51) Glacial silt, single layer, Iowa.
- Figure 469 (I—52) Glacial silt, single layer, Iowa.
- Figure 470 (I—53) Glacial silt, single layer, Iowa.
- Figure 471 (I—54) Glacial silt, single layer, Iowa.
- Figure 472 (I—55) Glacial silt, single layer, Iowa.

Bankland Silt, Mississippi Delta

- Figure 473 (I—45) Silt, Louisiana.
- Figure 474 (I—46) Silt, Louisiana.
- Figure 475 (I—78) Silt, Louisiana.

Natural Levee Sediments

- Figure 476 (XII— 13) Mississippi River.
- Figure 477 (XII— 89) Mississippi River.
- Figure 478 (XII—159) Mississippi River.
- Figure 479 (XII—230) Mississippi River.



Figures 465-479

PLATE XXXV

FLUVIAL SEDIMENTS

Silt from Small Streams

Figure 480 (I—70) Alluvium, Maryland.

Figure 481 (I—71) Silt, South Dakota.

Figure 482 (I—72) Alluvium, Maryland.

Figure 483 (I—73) Silt, Maryland.

Heavy Concentrates

Figure 484 (III—120) Olivine sand, rill channel, Oahu.

Figure 485 (III—523) Magnetite sand, rill channel, Oahu.

Figure 486 (XI—1543) Black sand, rill channel, Virginia.

Figure 487 (XI—1578) Black sand, rill channel, Virginia.

Figure 488 (I—338) Magnetite-Quartz sand, Texas.

Figure 489 (I—340) Magnetite-Quartz sand, Texas.

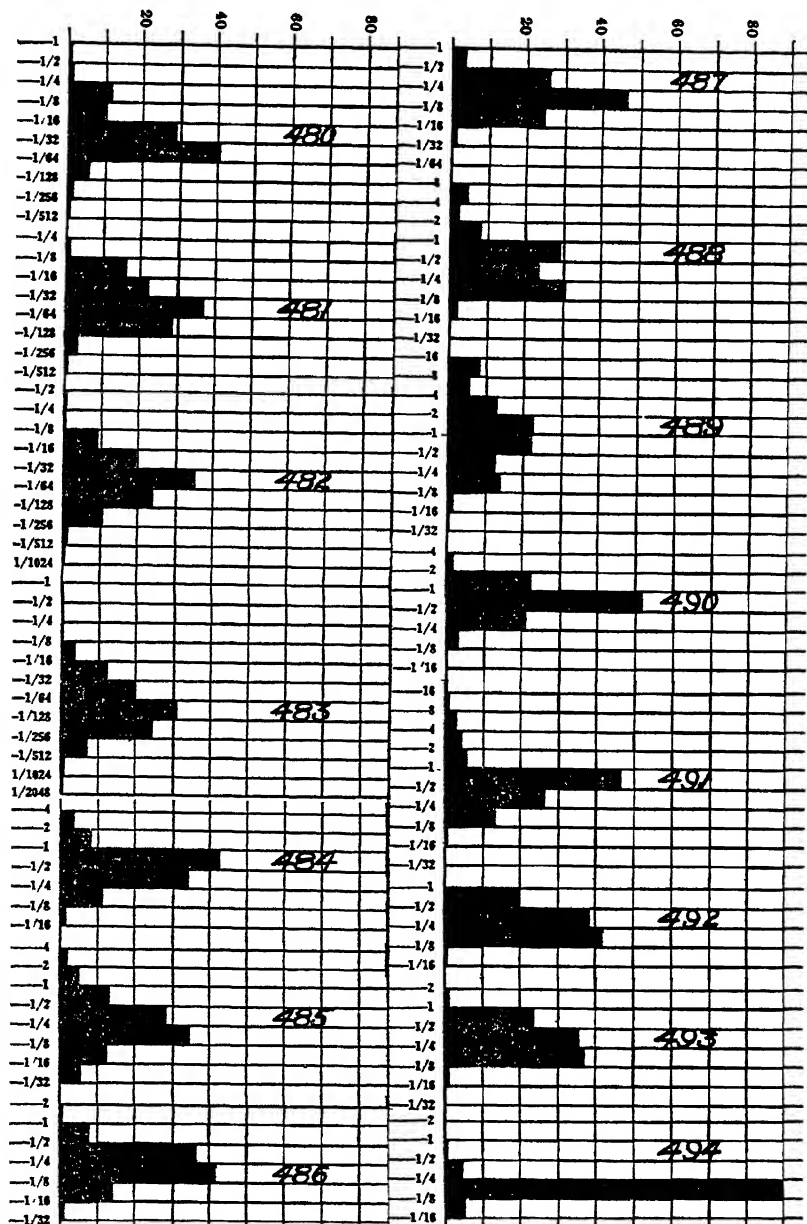
Figure 490 (I—343) Magnetite-Quartz sand, Texas.

Figure 491 (I—344) Magnetite-Quartz sand, Texas.

Figure 492 (I—345) Magnetite portion, No. 338, Texas.

Figure 493 (I—347) Magnetite portion, No. 340, Texas.

Figure 494 (I—350) Magnetite portion, No. 343, Texas.



Figures 480-494

PLATE XXXVI

FLUVIAL SEDIMENTS

Heavy Concentrates

Figure 495 (I—351) Magnetite portion, No. 344, Texas.

Ancient Fluvial Sediments

Figure 496 (II—74A) Gravel, Pleistocene terrace, Maryland.

Figure 497 (II—116M) Gravel, Wicomico terrace, D. C.

Figure 498 (II—133) Gravel, Brandywine terrace, D. C.

Figure 499 (II—138) Gravel, Sunderland terrace, D. C.

Figure 500 (II—146) Gravel, Tenley terrace, D. C.

Figure 501 (II—165T) Gravel, Tenley terrace, D. C.

Figure 502 (II—323) Gravel, Brandywine terrace, Maryland.

Figure 503 (II—329) Sand, Brandywine terrace, Maryland.

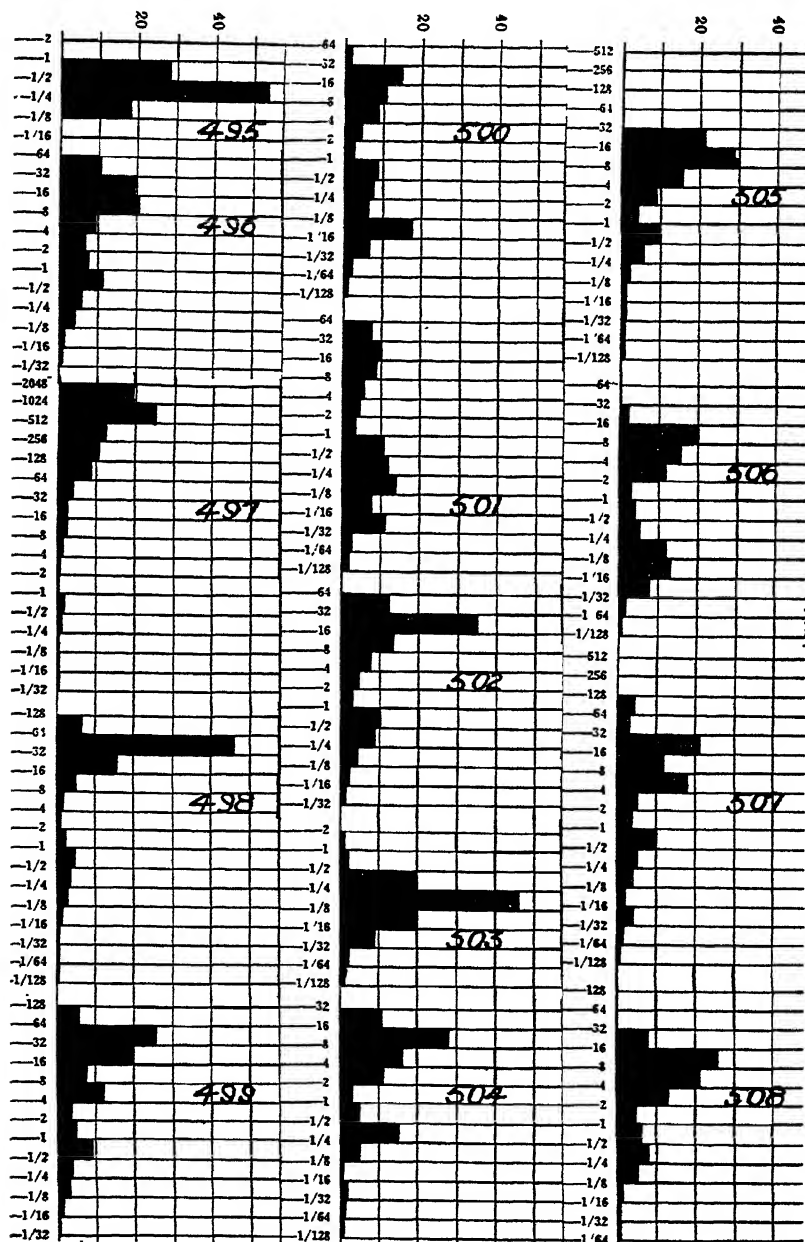
Figure 504 (II—330) Gravel, Brandywine terrace, Maryland.

Figure 505 (II—334F) Gravel, Brandywine terrace, Maryland.

Figure 506 (II—345) Gravel, Brandywine terrace, Maryland.

Figure 507 (II—379M) Gravel, Sunderland terrace, D. C.

Figure 508 (II—440B) Gravel, Sunderland terrace, D. C.



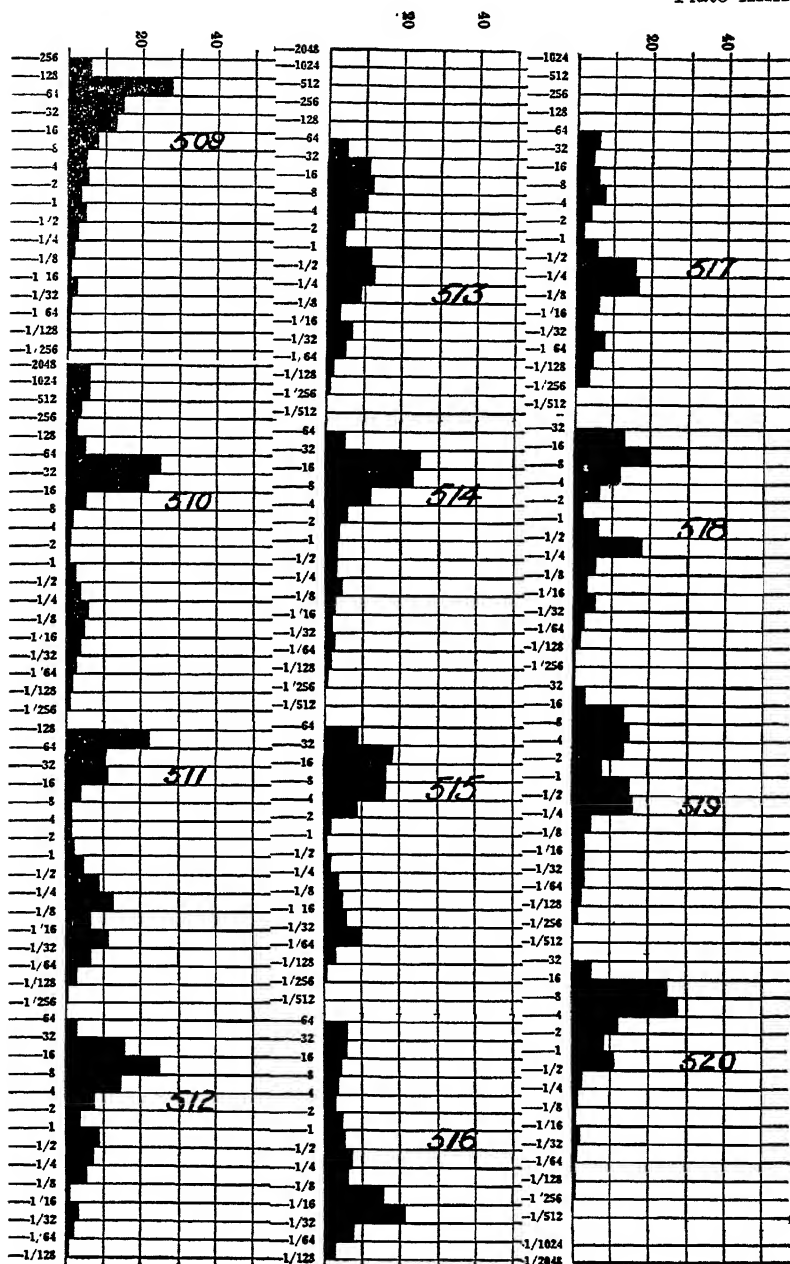
Figures 495-508

PLATE XXXVII

FLUVIAL SEDIMENTS

Ancient Fluvial Sediments

- Figure 509 (II—480A) Gravel, Sunderland terrace, Virginia.
Figure 510 (II—546) Gravel, Sunderland terrace, Maryland.
Figure 511 (II—571) Gravel, Pleistocene terrace, Virginia.
Figure 512 (II—579) Gravel, Sunderland terrace, Virginia.
Figure 513 (II—588) Gravel, Tenley terrace, Virginia.
Figure 514 (II—591) Gravel, Tenley terrace, Virginia.
Figure 515 (II—619) Gravel, Brandywine terrace, West Virginia.
Figure 516 (II—693) Gravel, Tenley terrace, Pennsylvania.
Figure 517 (II—702) Gravel, Tenley terrace, Pennsylvania.
Figure 518 (II—726) Gravel, Brandywine terrace, Pennsylvania.
Figure 519 (II—814) Gravel, Pleistocene terrace, Maryland.
Figure 520 (II—823) Gravel, Sunderland terrace, Maryland.



Figures 509-520

PLATE XXXVIII

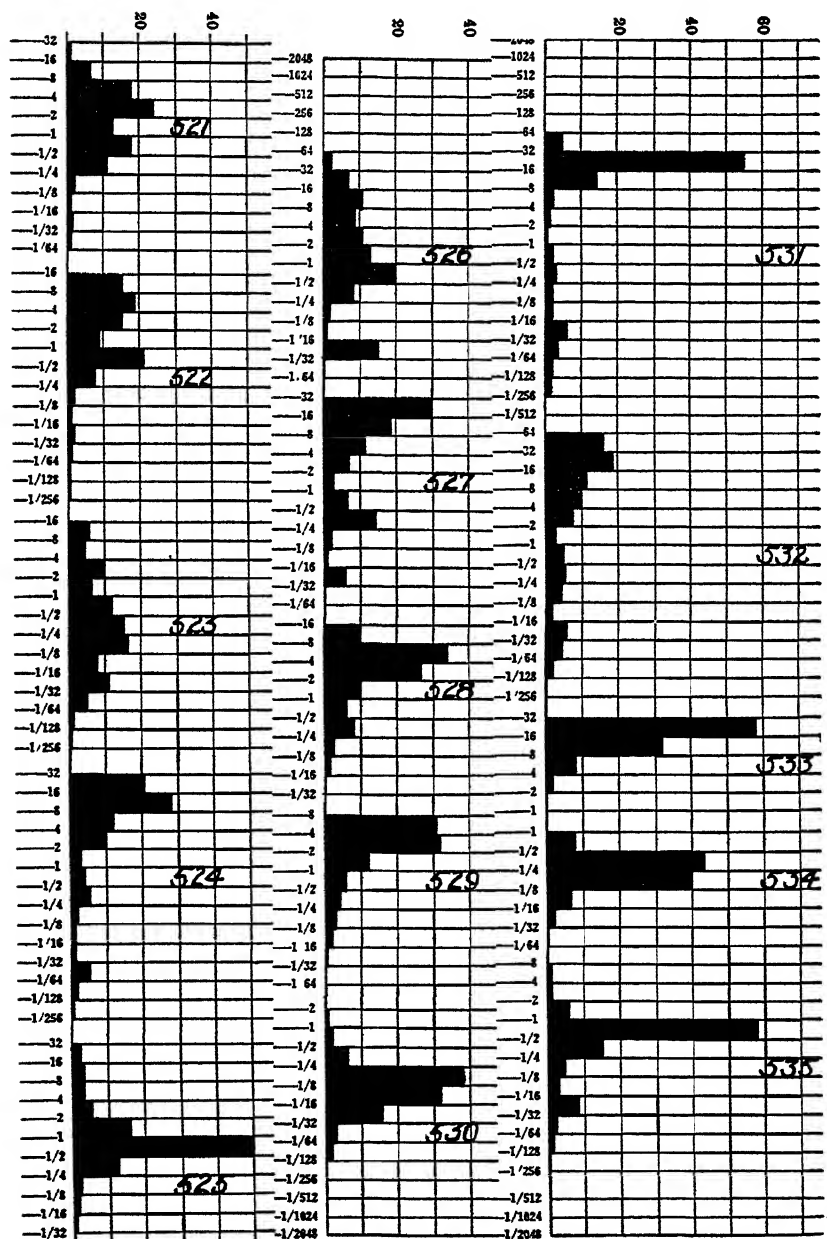
FLUVIAL SEDIMENTS

Ancient Fluvial Sediments

- Figure 521 (II—828) Gravel, Sunderland terrace, Maryland.
Figure 522 (II—848) Gravel, Sunderland terrace, Maryland.
Figure 523 (II—896) Gravel, Sunderland terrace, Virginia.
Figure 524 (II—983) Gravel, Sunderland terrace, Virginia.
Figure 525 (XI—1364) Gravel, Sunderland terrace, Virginia.
Figure 526 (XI—1387C) Gravel, Brandywine terrace, Virginia.
Figure 527 (XI—1444) Gravel, Brandywine terrace, Virginia.
Figure 528 (XI—1686) Gravel, Sunderland terrace, Virginia.
Figure 529 (XI—1999) Gravel, Pleistocene terrace, Virginia.

Ancient Sediments, Probably Mostly Fluvial but in Part
Possibly Deltaic or Littoral Marine'

- Figure 530 (II—130A) Sand, Patuxent formation, Maryland.
Figure 531 (II—164) Gravel, Patuxent formation, D. C.
Figure 532 (II—165) Gravel, Patuxent formation, D. C.
Figure 533 (II—167) Gravel, Patuxent formation, D. C.
Figure 534 (II—234) Sand, Patuxent formation, D. C.
Figure 535 (II—377C) Sand, Patuxent formation, D. C.



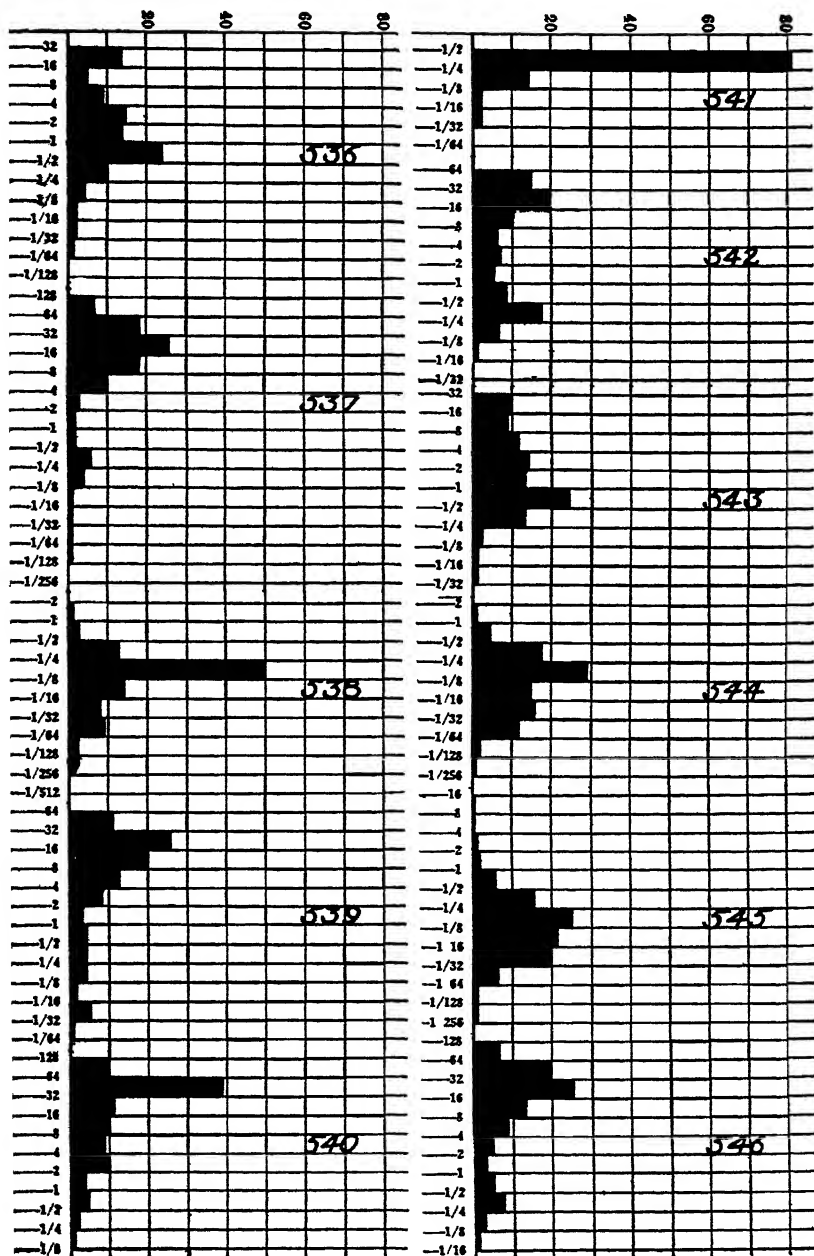
Figures 521-535

PLATE XXXIX

FLUVIAL SEDIMENTS

Ancient Sediments, Probably Mostly Fluvial but in Part
Possibly Deltaic or Littoral Marine¹

- Figure 536 (II—377E) Gravel, Patuxent formation, D. C.
Figure 537 (II—383) Gravel, Patuxent formation, D. C.
Figure 538 (II—977E) Sand, Patuxent formation, D. C.
Figure 539 (II—977K) Gravel, Patuxent formation, D. C.
Figure 540 (II—977X) Gravel, Patuxent formation, D. C.
Figure 541 (XI—1387A) Sand, Patuxent formation, Virginia.
Figure 542 (XI—1387B) Gravel, Patuxent formation, Virginia.
Figure 543 (XI—1434) Gravel, Patuxent formation, Virginia.
Figure 544 (II—984) Sand, Sunderland terrace, Virginia.
Figure 545 (II—1009) Sand, Sunderland terrace, Virginia.
Figure 546 (II—45) Gravel, Pleistocene terrace, Maryland.



Figures 536-546

PLATE XL

FLUVIAL SEDIMENTS

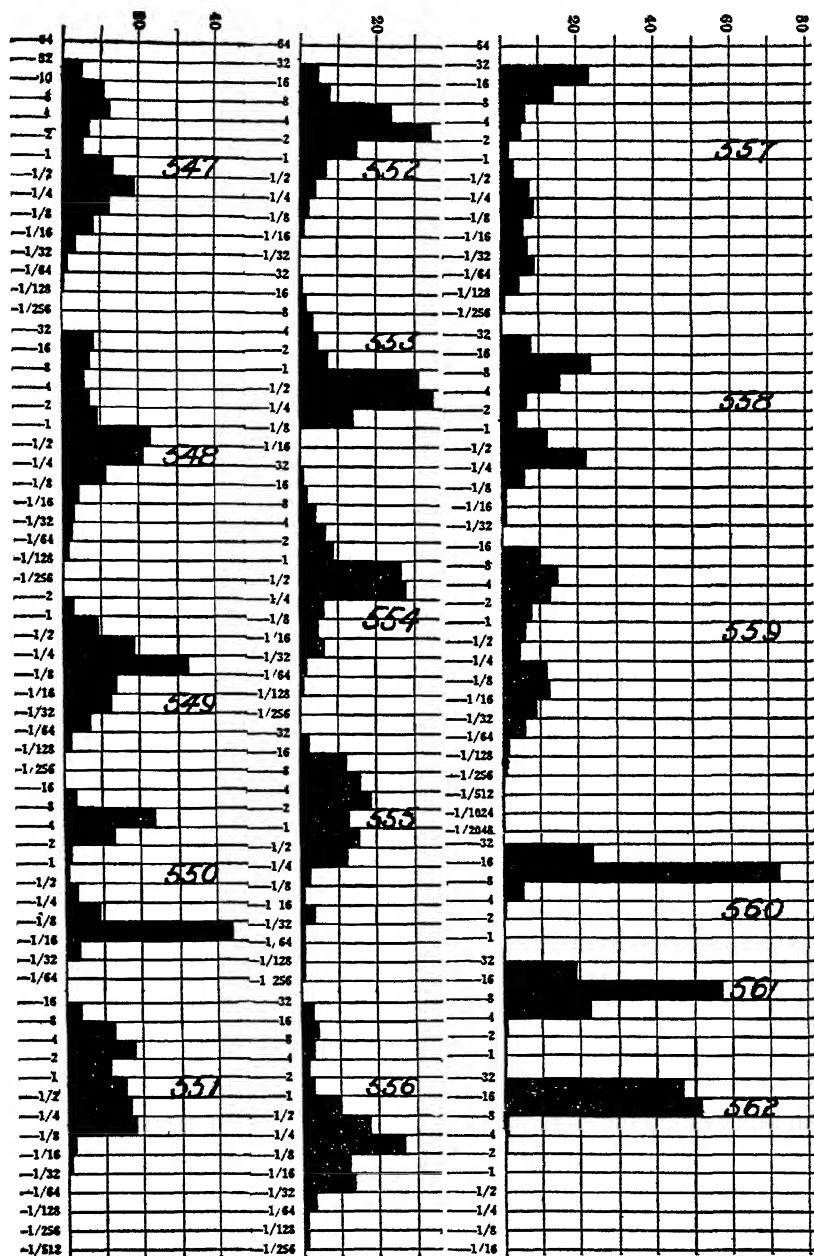
Ancient Sediments, Probably Mostly Fluvial but in Part
Possibly Deltaic or Littoral Marine

- Figure 547 (II—735A) Gravel, Pleistocene terrace, New
Jersey.
Figure 548 (II—735B) Gravel, Pleistocene terrace, New
Jersey.
Figure 549 (II—735C) Sand, Pleistocene terrace, New Jersey.
Figure 550 (II—736) Gravel, Pleistocene terrace, New Jersey.
Figure 551 (II—830) Gravel, Pleistocene terrace, Maryland.
Figure 552 (II—838) Gravel, Pleistocene terrace, Maryland.
Figure 553 (II—841) Sand, Pleistocene terrace, Maryland.
Figure 554 (II—995A) Sand, Pleistocene terrace, Virginia.
Figure 555 (II—995B) Gravel, Pleistocene terrace, Virginia.
Figure 556 (II—1000) Gravel, Pleistocene terrace, Virginia.
Figure 557 (II—1022) Gravel, Pleistocene terrace, Maryland.
Figure 558 (II—1042) Gravel, Pleistocene terrace, Maryland.
Figure 559 (II—1043) Gravel, Pleistocene terrace, Maryland.

MARINE SEDIMENTS

Beach Gravel

- Figure 560 (I—114) Beach gravel, Texas.
Figure 561 (I—115) Beach gravel, Massachusetts.
Figure 562 (I—116) Beach gravel, Texas.



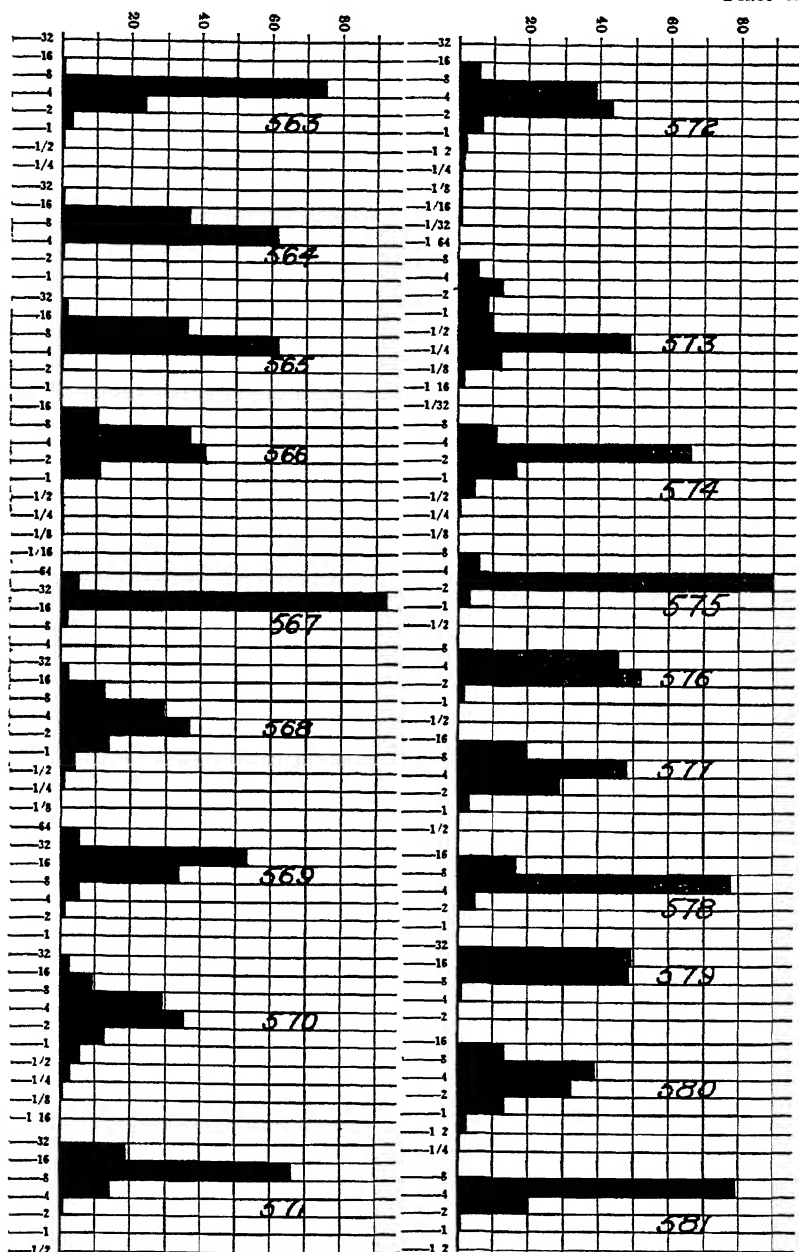
Figures 547-562

PLATE XLI

MARINE SEDIMENTS

Beach Gravel

- Figure 563 (I—117) Beach gravel, Alaska.
Figure 564 (I—118) Beach gravel, Texas.
Figure 565 (I—119) Beach gravel, Texas.
Figure 566 (I—120) Beach gravel, Alaska.
Figure 567 (II—731) Beach gravel, Massachusetts.
Figure 568 (II—733R) Beach gravel, Massachusetts.
Figure 569 (II—733R2) Beach gravel, Massachusetts.
Figure 570 (II—820) Beach gravel, Virginia.
Figure 571 (II—843) Beach gravel, Maryland.
Figure 572 (II—1055C) Beach gravel, Maryland
Figure 573 (XI—1747A) Beach gravel, Virginia.
Figure 574 (XI—1930E) Beach gravel, Virginia.
Figure 575 (III—1887) Beach gravel, Island of Oahu.
Figure 576 (III—1933) Beach gravel, Island of Oahu.
Figure 577 (IV—2505C) Beach gravel, Fanning Island.
Figure 578 (IV—2511) Beach gravel, composed of whole gastropod shells, Xmas Island.
Figure 579 (IV—2530) Beach gravel, Xmas Island.
Figure 580 (IV—2555H) Beach gravel, Xmas Island.
Figure 581 (IV—2556I) Beach gravel, Jarvis Island.



Figures 563-581

PLATE XLII

MARINE SEDIMENTS

Beach Gravel

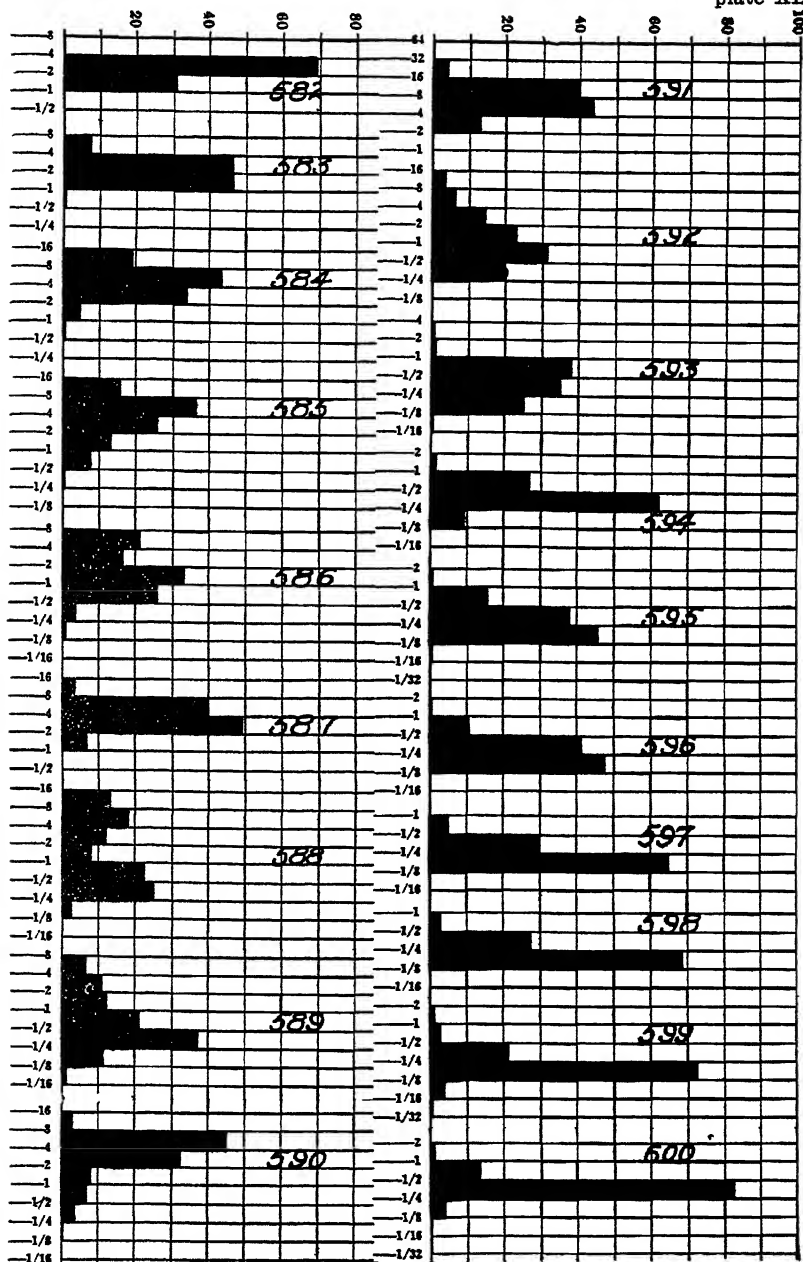
- Figure 582 (IV—2556L) Beach gravel, Jarvis Island.
Figure 583 (IV—2571C) Beach gravel, Washington Island.
Figure 584 (IV—2574D) Beach gravel, Washington Island.
Figure 585 (IV—2574H) Beach gravel, Washington Island.

Beach Lag Materials

- Figure 586 (IV—2527) Lag gravel on beach, sorted partly by
wind, partly by crabs, Xmas Island.
Figure 587 (IV—2528) Lag gravel from wave wash, Xmas
Island.
Figure 588 (IV—2536) Lag gravel from wave wash, Xmas
Island.
Figure 589 (XI—1874A) Sand, Virginia.
Figure 590 (XI—1951B) Gravel, Virginia.
Figure 591 (XI—2061A) Gravel, Virginia.
Figure 592 (XI—2286B) Gravel, Virginia.

Beach Sand

- Figure 593 (I—105) Sand, lake beach, Lake Michigan.
Figure 594 (I—106) Sand, lake beach, Lake Michigan.
Figure 595 (I—107) Sand, lake beach, Lake Michigan.
Figure 596 (I—108) Sand, lake beach, Lake Michigan.
Figure 597 (I—109) Sand, lake beach, Lake Michigan.
Figure 598 (I—110) Sand, lake beach, Lake Michigan.
Figure 599 (II—732B) Beach sand, Massachusetts.
Figure 600 (II—741A) Beach sand (see Dune Sand II—741B)
New Jersey.



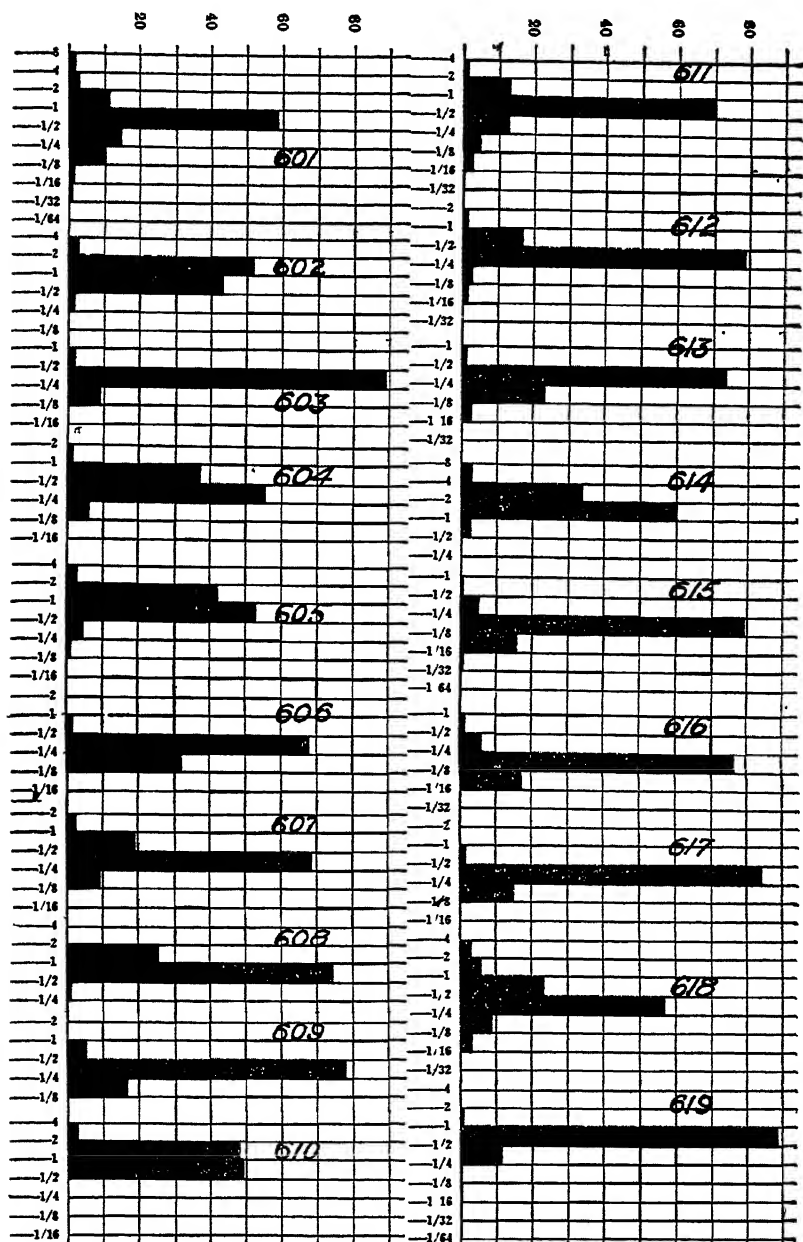
Figures 582-600

PLATE XLIII

MARINE SEDIMENTS

Beach Sand

- Figure 601 (II—1002) Beach sand, Maryland.
Figure 602 (III—12) Beach sand, Island of Oahu.
Figure 603 (III—21B) Beach sand, Island of Oahu.
Figure 604 (III—130) Beach sand, Island of Oahu.
Figure 605 (III—610) Beach sand, Island of Oahu.
Figure 606 (III—611) Beach sand, Island of Oahu.
Figure 607 (III—1302) Beach sand, Island of Oahu.
Figure 608 (III—1885) Beach sand, Island of Oahu.
Figure 609 (III—1886) Beach sand, Island of Oahu.
Figure 610 (III—2027) Beach sand, Island of Oahu.
Figure 611 (VII—30) Beach sand, California.
Figure 612 (XI—1738) Beach sand, Virginia.
Figure 613 (XI—1747C) Beach sand, Virginia.
Figure 614 (XI—1749) Beach sand, Virginia.
Figure 615 (XI—1799) Beach sand, Virginia.
Figure 616 (XI—1874B) Beach sand, Virginia.
Figure 617 (XI—1874C) Beach sand, Virginia.
Figure 618 (XI—1950) Beach sand, Virginia.
Figure 619 (XI—2061B) Beach sand, Virginia.



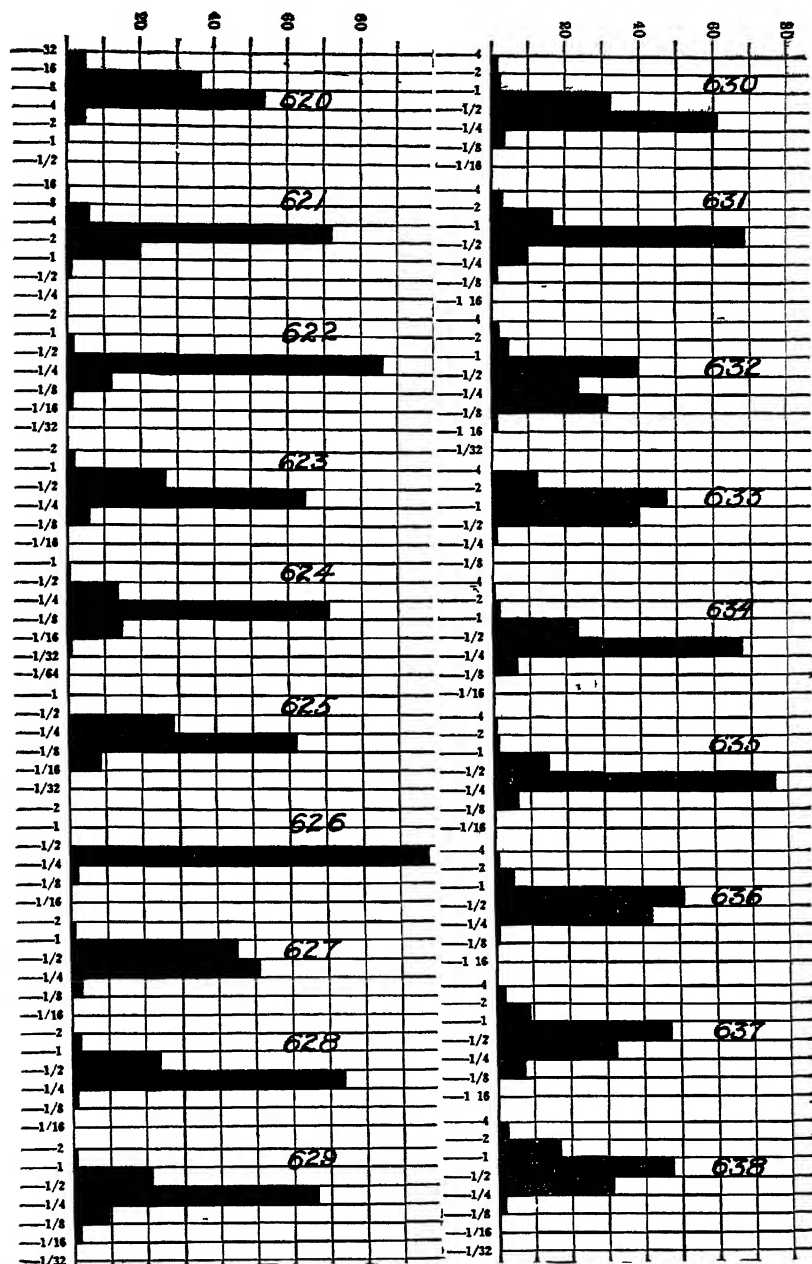
Figures 601-619

PLATE XLIV

MARINE SEDIMENTS

Beach Sand

- Figure 620 (XI—2071A) Beach sand, Virginia.
Figure 621 (XI—2071B) Beach sand, Virginia.
Figure 622 (XI—2071C) Beach sand, Virginia.
Figure 623 (XI—2072A) Beach sand (see Dune sand, XI-2072B), Virginia.
Figure 624 (XI—2073) Beach sand, Virginia.
Figure 625 (XI—2075) Beach sand, Virginia.
Figure 626 (XI—2254B) Beach sand, Virginia.
Figure 627 (XI—2277B) Beach sand, Virginia.
Figure 628 (XI—2286A) Beach sand, Virginia.
Figure 629 (XI—2288) Beach sand, Virginia.
Figure 630 (IV—X) Beach sand, Xmas Island.
Figure 631 (IV—2501) Beach sand, Fanning Island.
Figure 632 (IV—2517B) Beach sand, Xmas Island.
Figure 633 (IV—2529) Beach sand, Xmas Island.
Figure 634 (IV—2537) Beach sand, Xmas Island.
Figure 635 (IV—2538) Beach sand, Xmas Island.
Figure 636 (IV—2546A) Beach sand, Xmas Island.
Figure 637 (IV—2551) Beach sand, Xmas Island.
Figure 638 (IV—2556F) Beach sand, Jarvis Island.



Figures 620-638

PLATE XLV

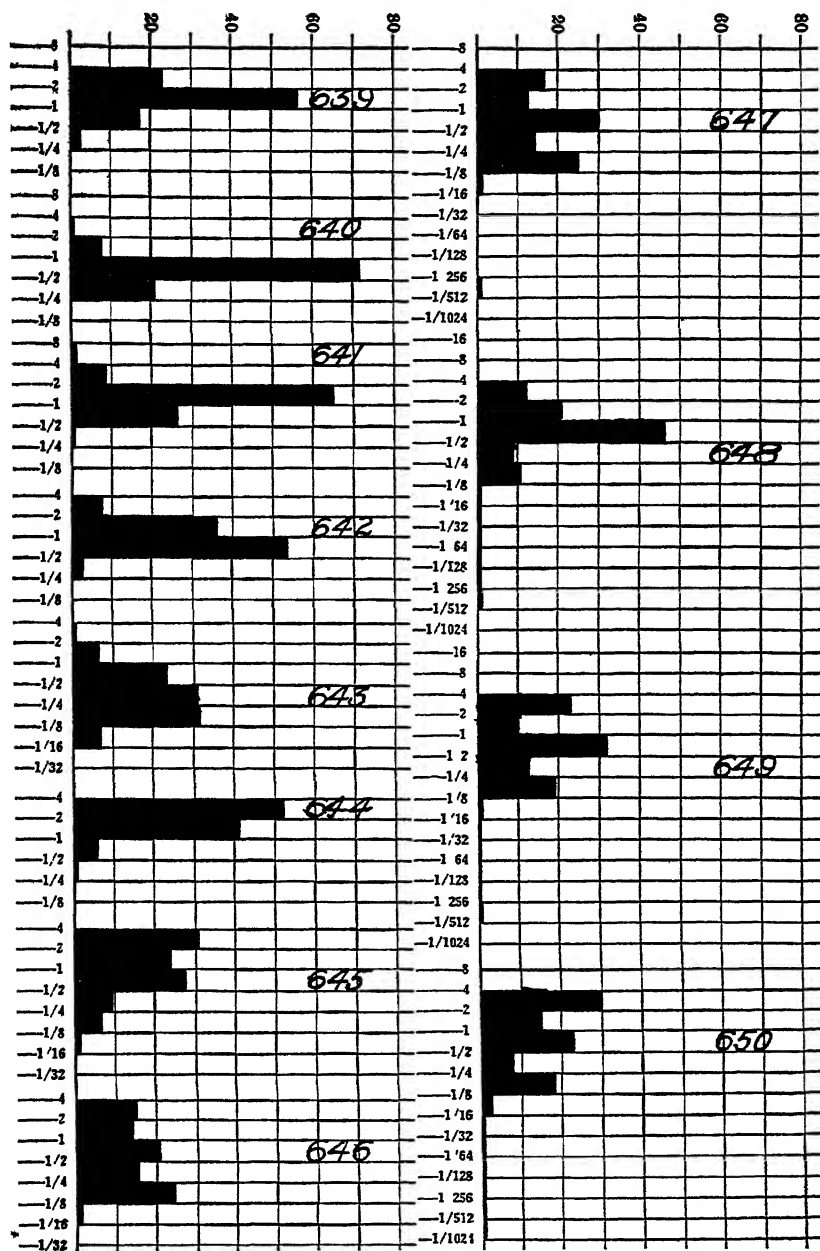
MARINE SEDIMENTS

Beach Sand

- Figure 639 (IV—2556J) Beach sand, Jarvis Island.
Figure 640 (IV—2572A) Beach sand, Washington Island.
Figure 641 (IV—2572F) Beach sand, Washington Island.
Figure 642 (IV—2573A) Beach sand, Washington Island.

Shallow Water Sediments

- Figure 643 (XIII—Aua 1) Beach sand, Samoa.
Figure 644 (XIII—Aua 2) Beach gravel, Samoa.
Figure 645 (XIII—Aua 3) Sand, 10 ft. from shore, Samoa.
Figure 646 (XIII—Aua 4) Sand, 50 ft. from shore, Samoa.
Figure 647 (XIII—Aua 5) Sand, 100 ft. from shore, Samoa.
Figure 648 (XIII—Aua 6) Sand, 200 ft. from shore, Samoa.
Figure 649 (XIII—Aua 7) Sand, 300 ft. from shore, Samoa.
Figure 650 (XIII—Aua 8) Sand, 400 ft. from shore, Samoa.



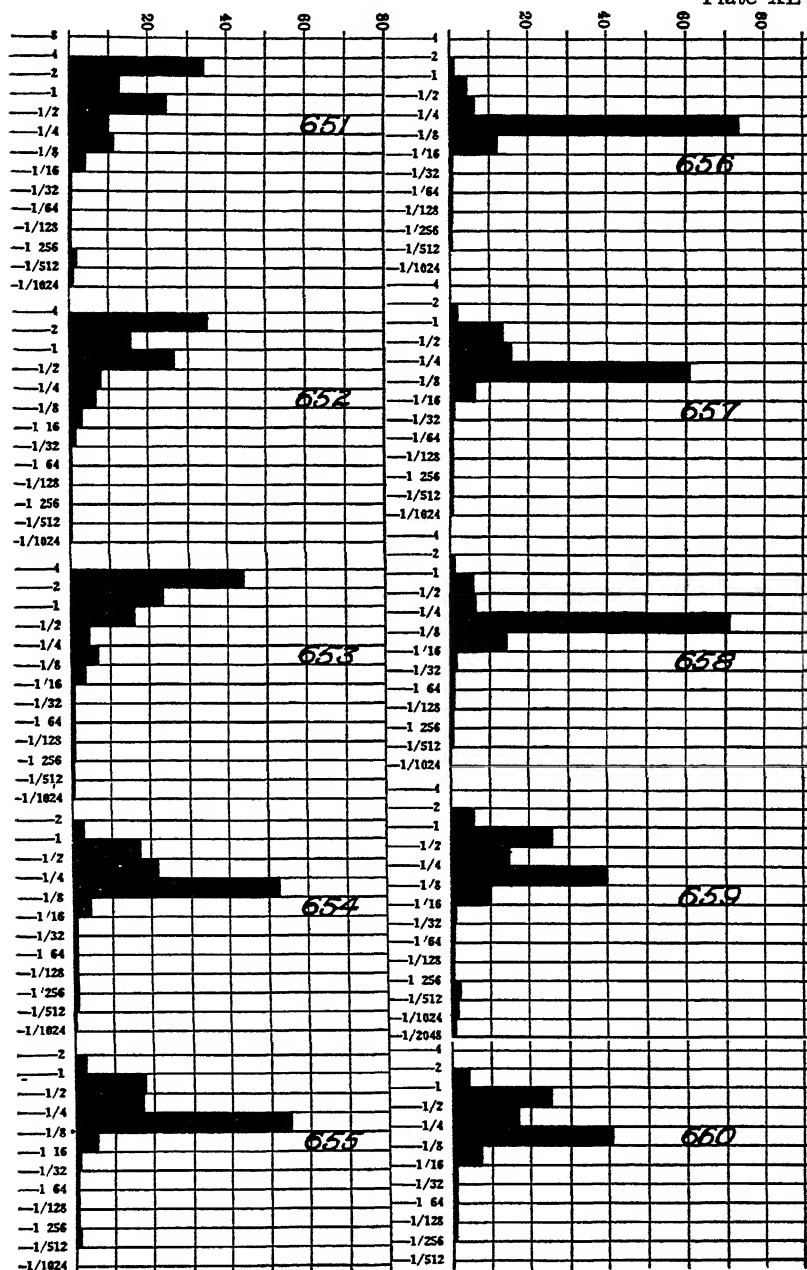
Figures 639-6

PLATE XLVI

MARINE SEDIMENTS

Shallow Water Sediments

- Figure 651 (XIII—Aua 9) Sand, 500 ft. from shore, Samoa.
Figure 652 (XIII—Aua 10) Sand, 600 ft. from shore, Samoa.
Figure 653 (XIII—Aua 11) Sand, 700 ft. from shore, Samoa.
Figure 654 (XIII—Aua 20) Sand, off reef front, Samoa.
Figure 655 (XIII—Aua 21) Sand, off reef front, Samoa.
Figure 656 (XIII—Aua 22) Sand, off reef front, Samoa.
Figure 657 (XIII—Aua 23) Sand, off reef front, Samoa.
Figure 658 (XIII—Aua 24) Sand, off reef front, Samoa.
Figure 659 (XIII—Nuuli A) Sand, center of lagoon, Samoa.
Figure 660 (XIII—Nuuli B) Sand, center of lagoon, Samoa.



Figures 651-660

PLATE XLVII

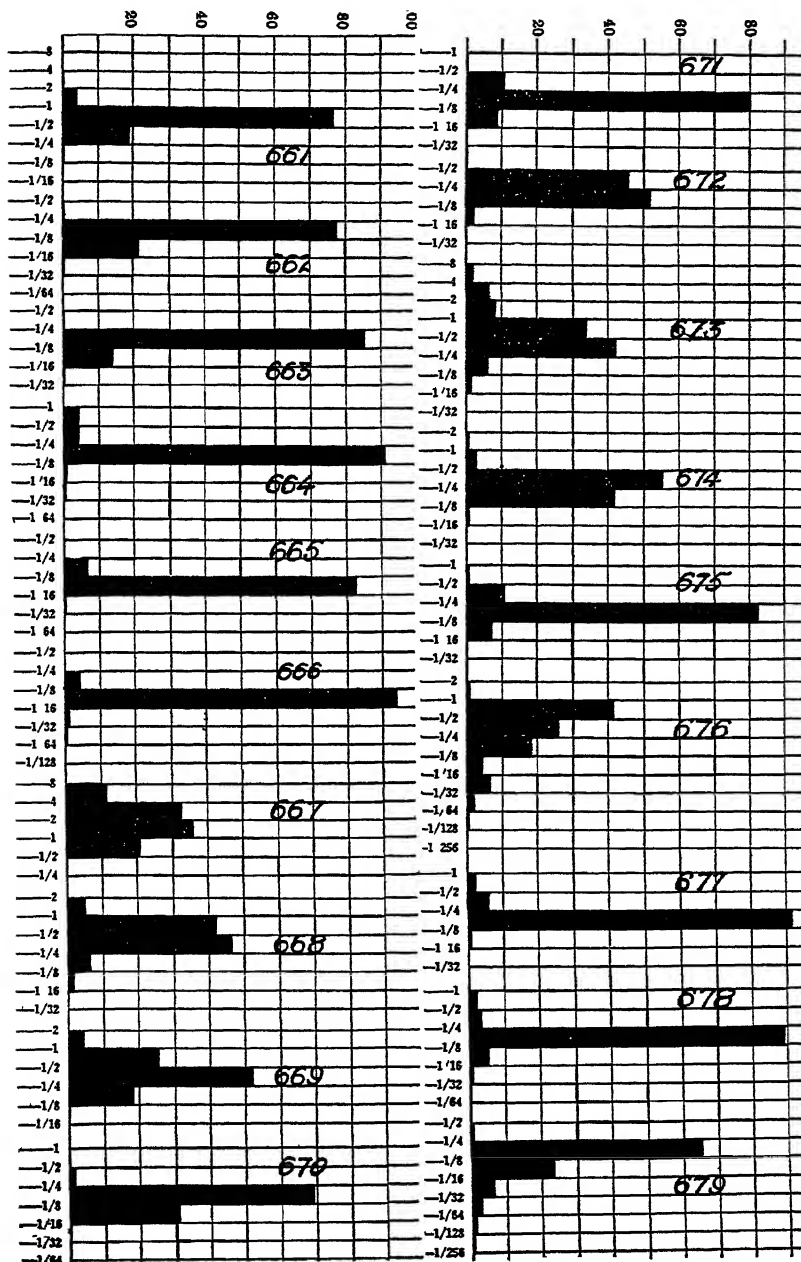
MARINE SEDIMENTS

Heavy Concentrates

- Figure 661 (I—339) Magnetite-quartz sand, Lake Michigan beach.
- Figure 662 (I—341) Magnetite-quartz sand, Ocean beach, Texas.
- Figure 663 (I—342) Magnetite-quartz sand, Ocean beach, Texas.
- Figure 664 (I—346) Magnetite portion of 339
- Figure 665 (I—348) Magnetite portion of 341.
- Figure 666 (I—349) Magnetite portion of 342.
- Figure 667 (III—740D) Olivine-augite sand, Island of Oahu.
- Figure 668 (III—796) Heavy sand, Island of Oahu.
- Figure 669 (III—1021) Heavy sand, Island of Oahu.
- Figure 670 (II—1018) Black beach sand, Maryland.
- Figure 671 (XI—1579A) Black beach sand, Virginia.
- Figure 672 (XI—1579B) Black beach sand, Virginia.
- Figure 673 (XI—1874D) Black beach sand, Virginia (contains light shell fragments also).
- Figure 674 (XI—1951C) Black beach sand, Virginia.
- Figure 675 (XI—2012) Black beach sand, Virginia.

Continental Shelf Sands

- Figure 676 (I—134) Sand and mud, inner shelf, North Atlantic.
- Figure 677 (I—135) Sand, inner shelf, Cuba.
- Figure 678 (I—136) Sand, inner shelf, Florida.
- Figure 679 (I—137) Sand, inner shelf, Labrador.



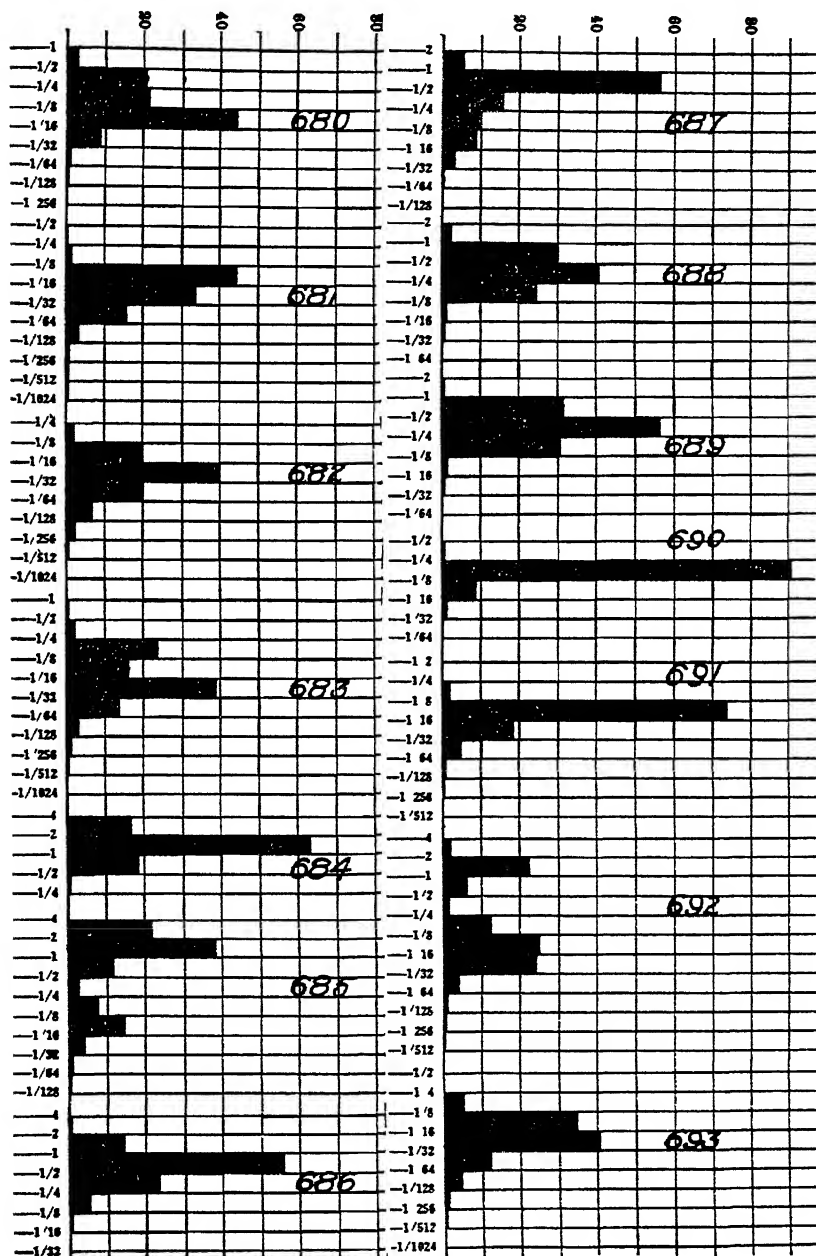
Figures 661-679

PLATE XLVIII

MARINE SEDIMENTS

Continental Shelf Sands

- Figure 680 (I—138) Sand and mud, inner shelf, North Atlantic.
- Figure 681 (I—139) Mud, inner shelf, Massachusetts.
- Figure 682 (I—140) Sand and mud, inner shelf, Cuba.
- Figure 683 (I—141) Sand and mud, inner shelf, Patagonia.
- Figure 684 (I—142) Sand, outer shelf, North Atlantic.
- Figure 685 (I—143) Sand, outer shelf, North Atlantic.
- Figure 686 (I—144) Sand, outer shelf, North Atlantic.
- Figure 687 (I—145) Sand, outer shelf, North Atlantic.
- Figure 688 (I—146) Sand, outer shelf, Yucatan.
- Figure 689 (I—147) Sand, outer shelf, North Atlantic.
- Figure 690 (I—148) Sand, outer shelf, North Atlantic.
- Figure 691 (I—149) Sand and mud, outer shelf, North Atlantic.
- Figure 692 (I—150) Sand and mud, outer shelf, North Atlantic.
- Figure 693 (I—151) Sand and mud, outer shelf, North Atlantic.



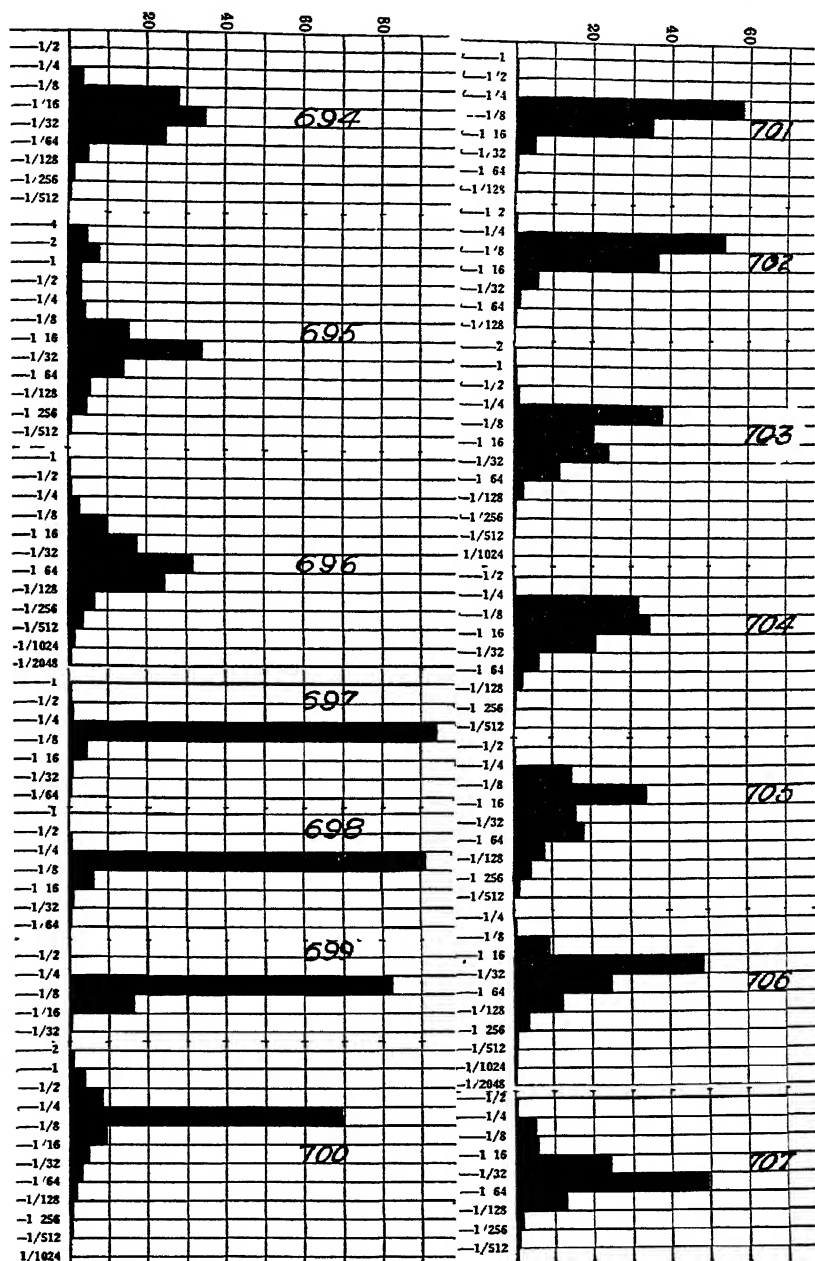
Figures 680-693

PLATE XLIX

MARINE SEDIMENTS

Continental Shelf Sands

- Figure 694 (I—152) Sand and mud, outer shelf, North Atlantic.
- Figure 695 (I—153) Sand and mud, outer shelf, North Atlantic.
- Figure 696 (I—154) Mud, outer shelf, North Atlantic.
- Figure 697 (I—165) Sand, marine shelf, Bering Sea.
- Figure 698 (I—166) Sand, marine shelf, Bering Sea.
- Figure 699 (I—167) Sand, marine shelf, Bering Sea.
- Figure 700 (I—168) Sand, marine shelf, Bering Sea.
- Figure 701 (I—169) Sand, marine shelf, Bering Sea.
- Figure 702 (I—170) Sand and mud, marine shelf, Bering Sea.
- Figure 703 (I—171) Sand and mud, marine shelf, Bering Sea.
- Figure 704 (I—172) Sand and mud, marine shelf, Bering Sea.
- Figure 705 (I—173) Sand and mud, marine shelf, Bering Sea.
- Figure 706 (I—174) Sand and mud, marine shelf, Alaskan Coast.
- Figure 707 (I—175) Sand and mud, marine shelf, Alaskan Coast.



Figures 694-707

PLATE L

MARINE SEDIMENTS

Steep Submerged Continental Slope Sediments

Figure 708 (I—155) Marine sand and mud, California.

Figure 709 (I—156) Marine sand, Washington.

Figure 710 (I—157) Marine sand and mud, California.

Figure 711 (I—158) Marine sand and mud, California.

Figure 712 (I—159) Marine sand, Washington.

Figure 713 (I—160) Marine mud, California.

Figure 714 (I—161) Marine green mud, California.

Figure 715 (I—162) Marine green mud, Lower California.

Figure 716 (I—163) Marine green mud, California.

Figure 717 (I—164) Marine offshore brown ooze, Washington.

Sediments from Margins of Ocean Basins

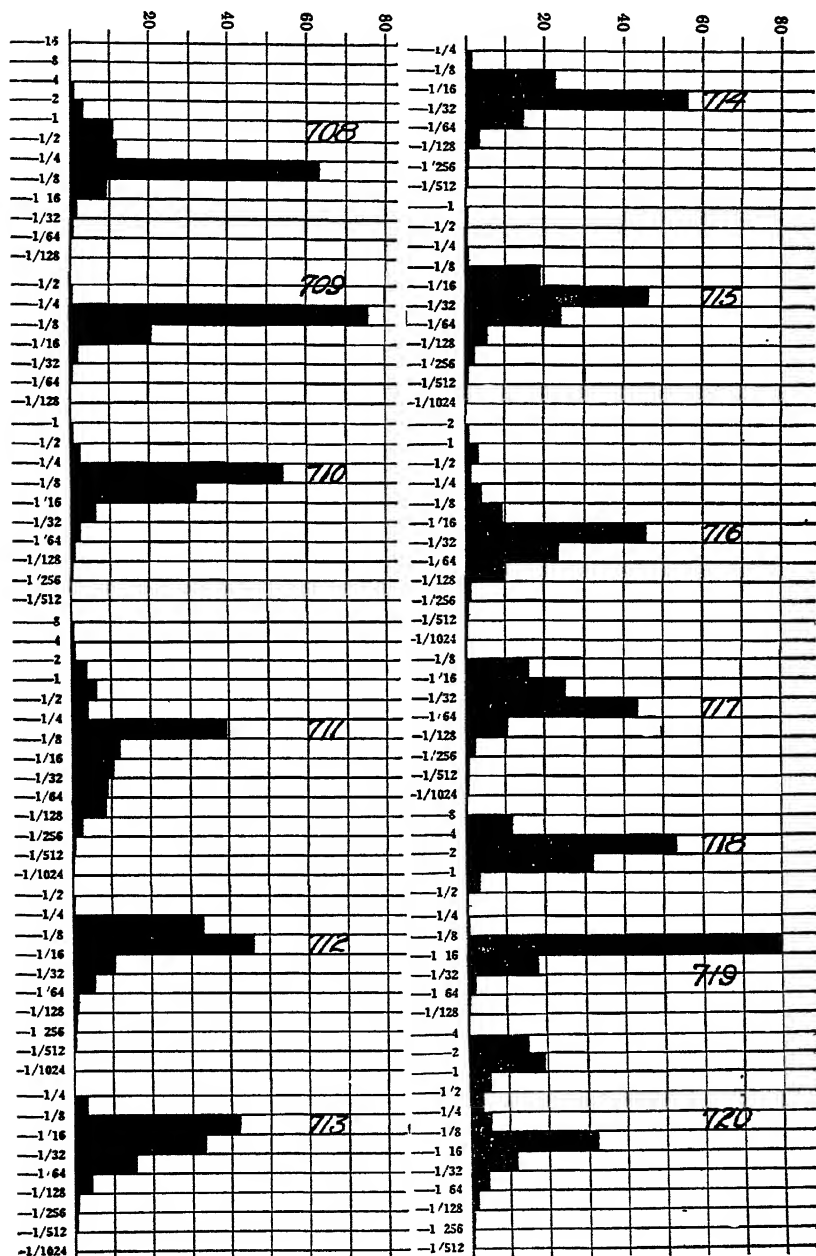
Figure 718 (I—182) Coral sand, 634 fathoms, Galapagos Islands.

Figure 719 (I—183) Brown ooze, 1753 fathoms (see reference).

Figure 720 (I—184) Soft green mud, 841 fathoms (see reference).

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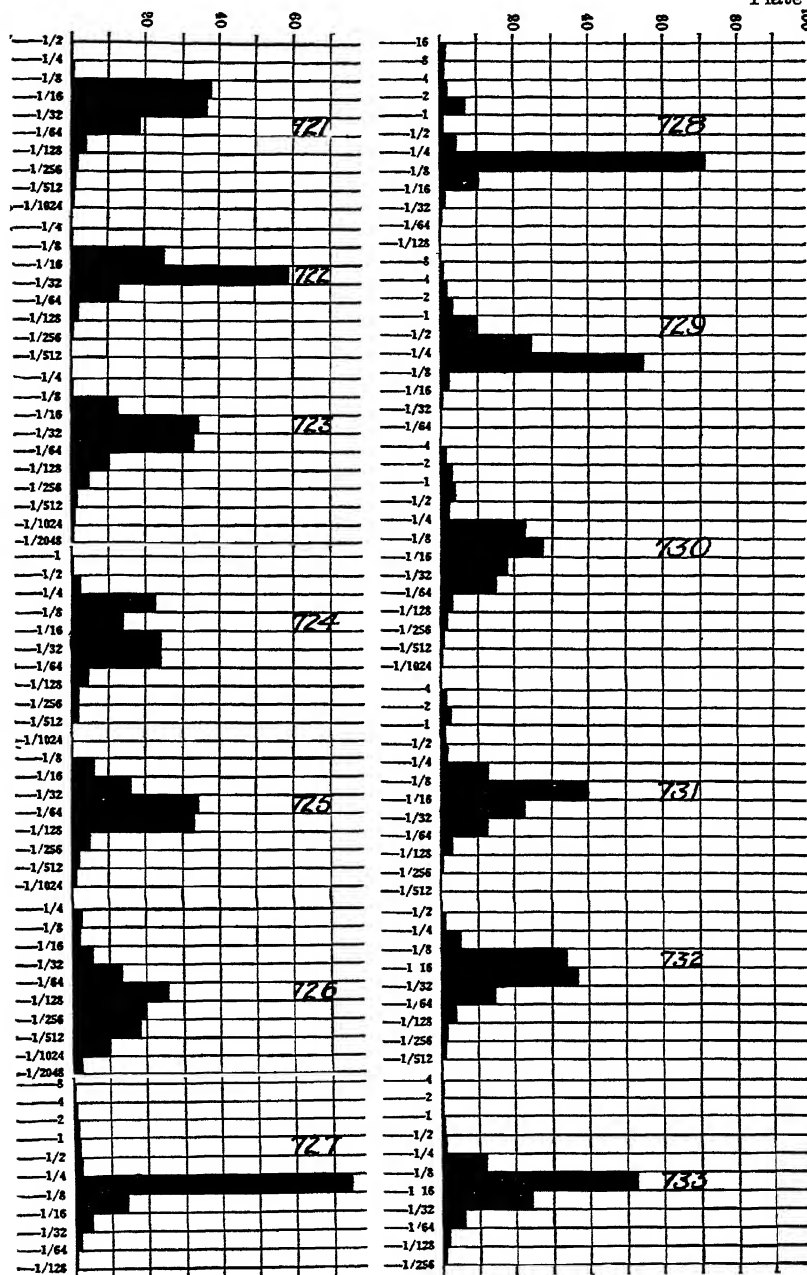
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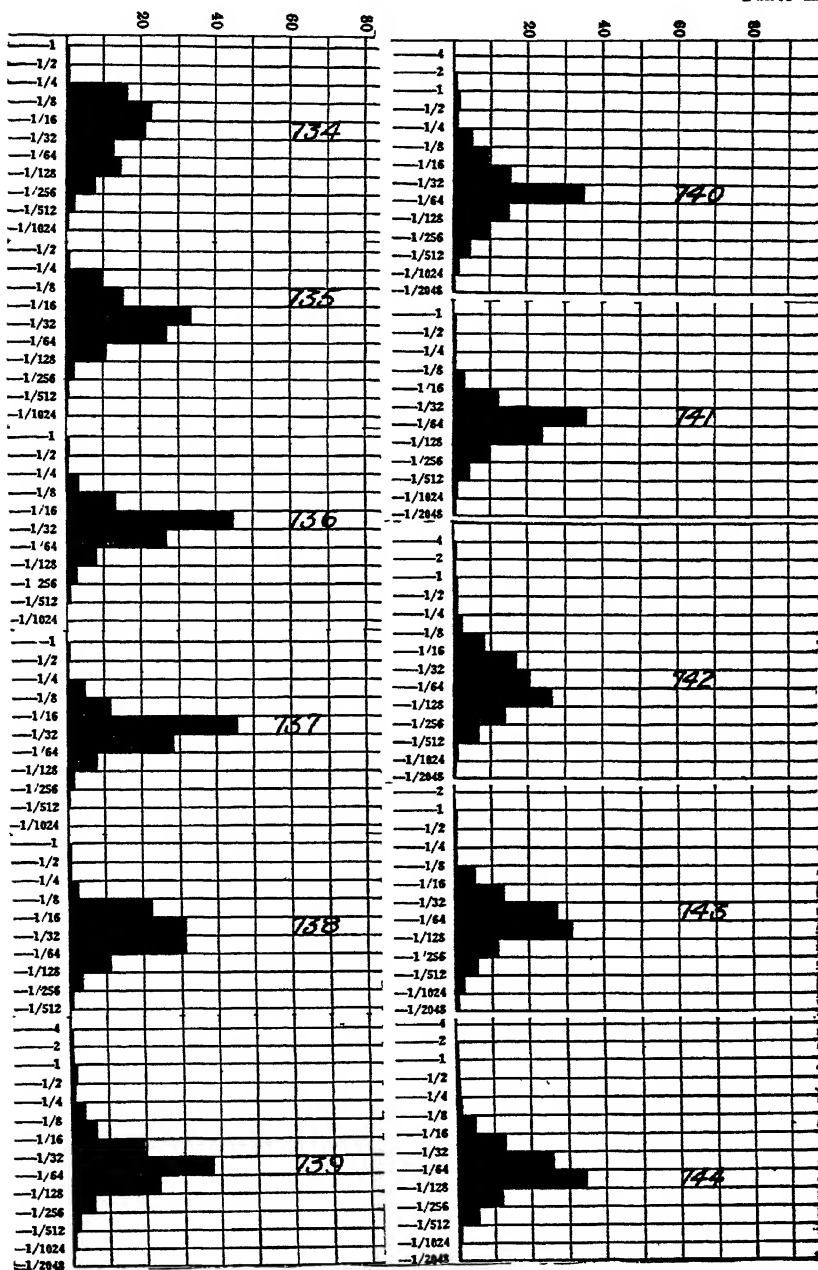
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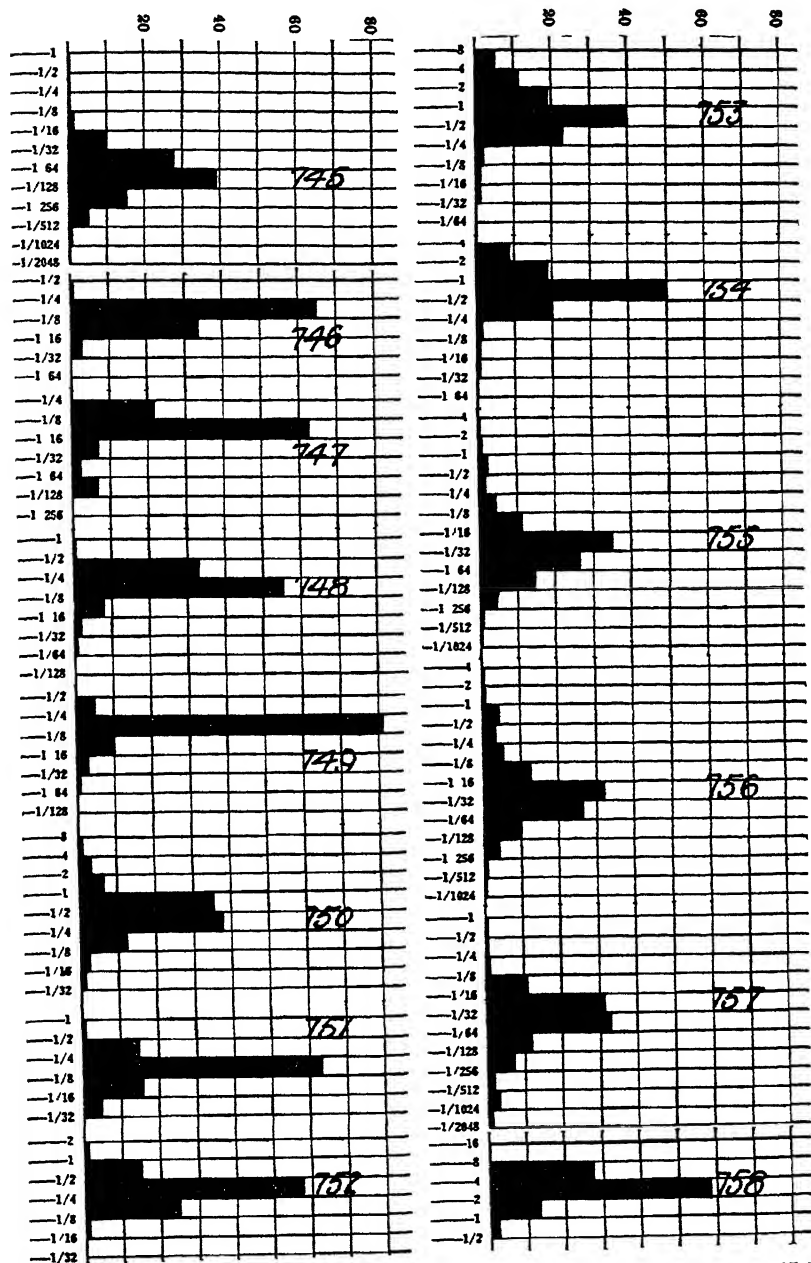
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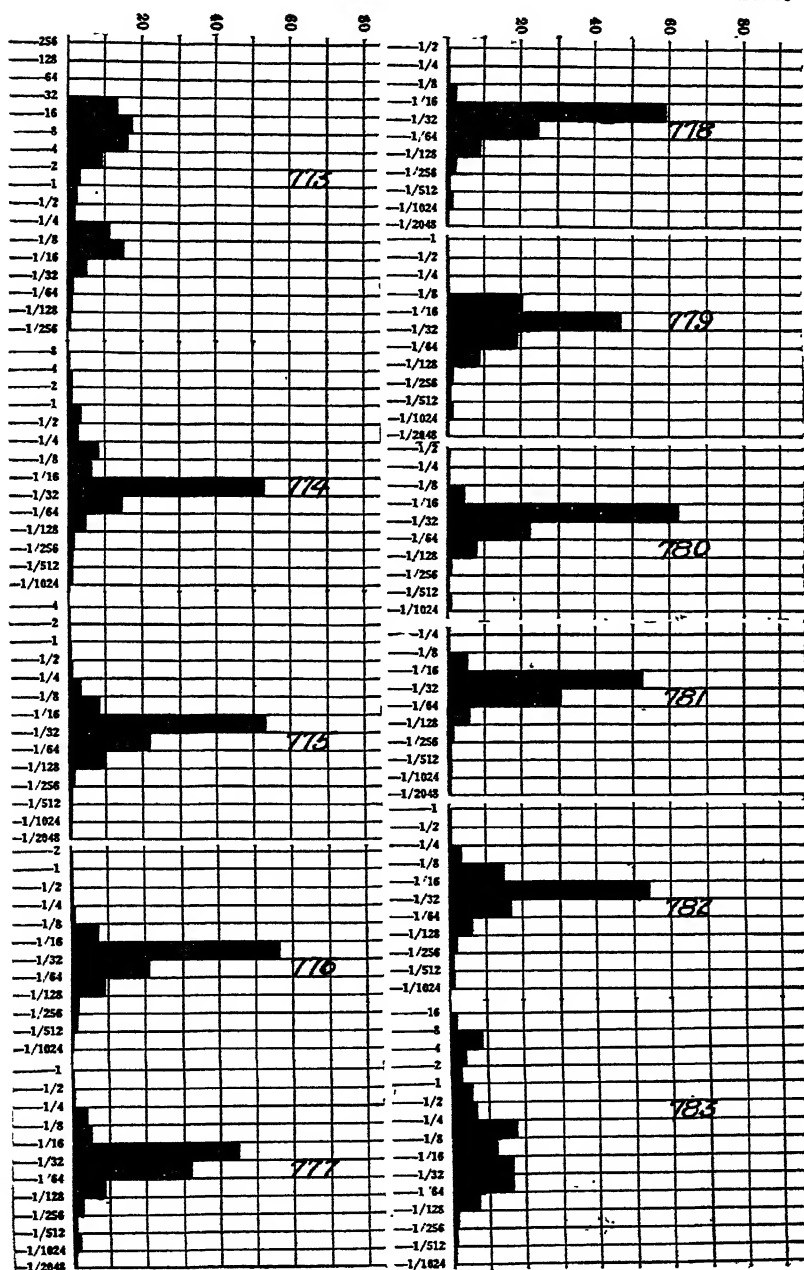


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GLACIAL SEDIMENTS

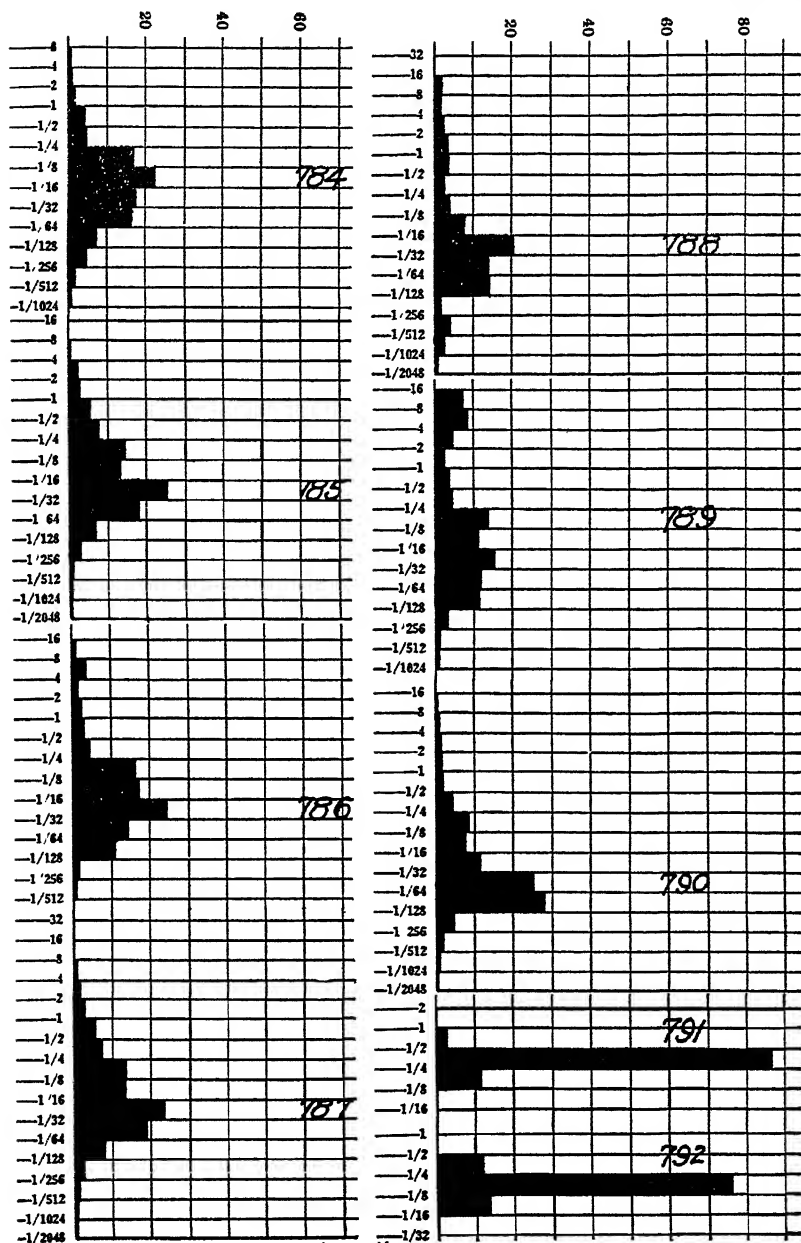
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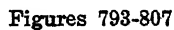
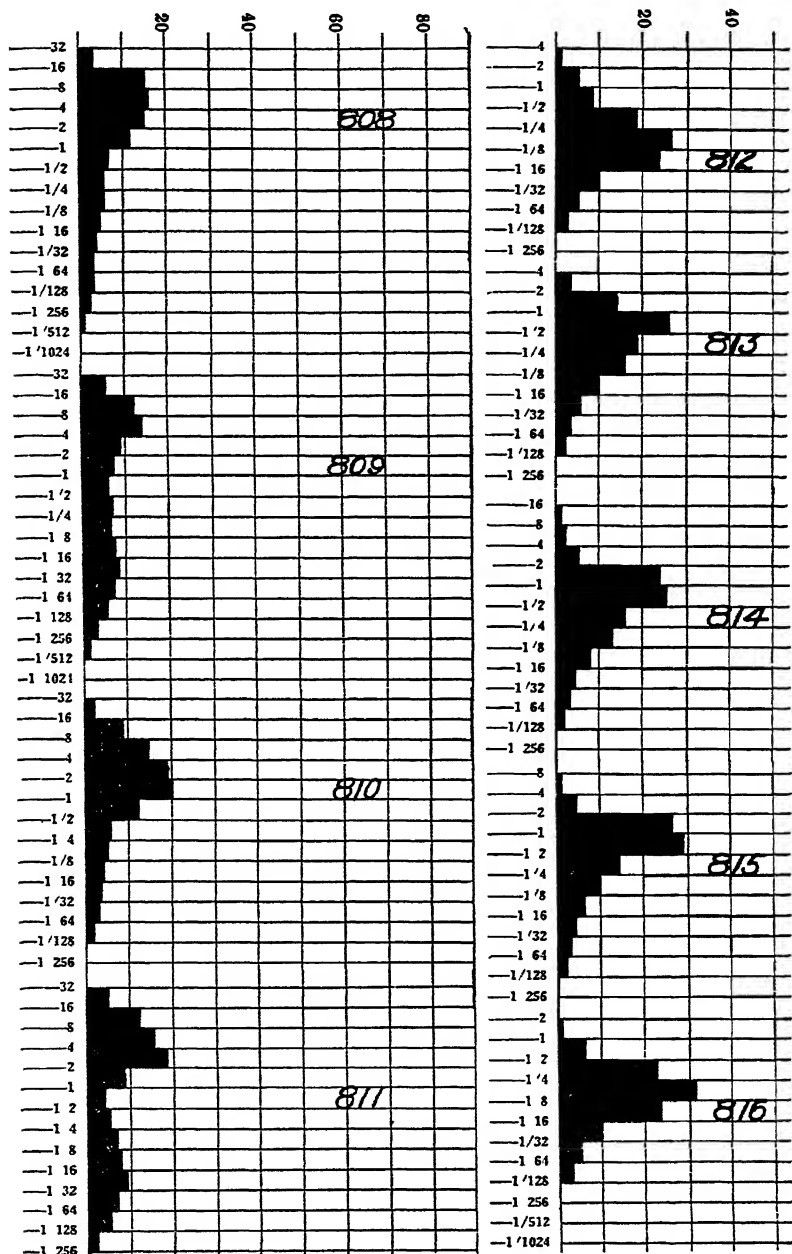


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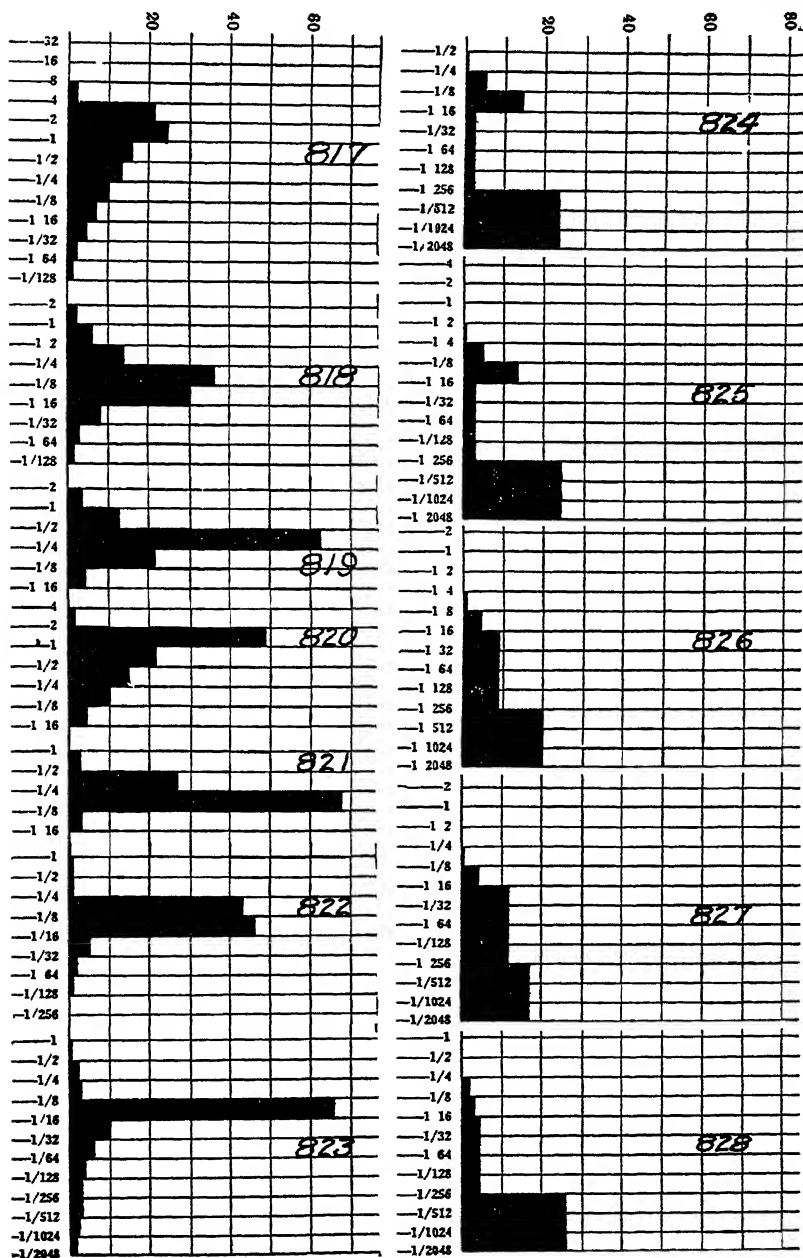
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THE MIXOCHOANITIC CEPHALOPODS

by

A. K. MILLER

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The Mixochoanitic Cephalopods

INTRODUCTION

The classification of the nautiloid cephalopods is not in as satisfactory condition as is that of most of the other major groups of fossil invertebrates. The earlier paleontologists attributed great importance to the external form of the shell, and they distinguished such groups as *longicones* and *brevicones*, and such genera as *Orthoceras*, *Cyrtoceras*, *Gyroceras*, *Gomphoceras*, *Trochoceras*, *Lituities*, etc.—all based on the shape of the conch. Barrande recognized that the structure of the siphuncle, the shape of the aperture, etc. were significant, but he considered them as subordinate in importance to the general form of the conch. Zittel followed Barrande, and it remained for Hyatt to establish a genetic classification and emphasize that “the general form and involution of the shell” are “relatively minor characters” and that surer guides to the affinities of the species and genera are to be found in “coincidence of structure, outlines of the aperture, and especially resemblances in developmental stages.”

In the Zittel-Eastman *Text-book Palaeontology* (1900) Hyatt introduced a scheme of classification which followed the general principles outlined in his previous scheme (*Genera of Fossil Cephalopods*, 1883) but contained important modifications. A note by the translator in this volume (p. 592) tells us that “the classification and diagnoses are condensed from an exhaustive Monograph on fossil Cephalopods, at present still in MS., which embodies the results of his [Hyatt's] life-study.” Unfortunately, owing to Hyatt's untimely death, this monograph was never completed, and we must regard the published classification as a tentative one in which the major features of Hyatt's philosophy are outlined, but in which the details are still to be worked out. As such it has much to commend it in comparison to any of the other classifications that have appeared before or since the time of its publication, and it clearly demonstrates that Hyatt's grasp of the group as a whole was far superior to that of any of his predecessors or successors.

In America Hyatt's classification has been accepted ever since its appearance in 1900, but most European paleontologists failed to

recognize the value of this genetic classification and continued to adhere to the old artificial one. However, two of the outstanding Swedish students of nautiloids, Holm and Troedsson, accepted Hyatt's work with comparatively few reservations, and from the recent writings of Pompeckj, Schindewolf, and Teichert and the last editions of Zittel's *Grundzüge der Paläontologie* we see that the Germans also are regarding it favorably. Abel, however, concludes that Hyatt's scheme is only provisional and has recently accepted the classification of the paleobiologist Dacqué, which is based chiefly on the morphological features of the siphuncle.

On the basis of the construction of the siphuncle and related structures, features which are more resistant to adaptation than is the external form of the shell, Hyatt (somewhat as Saemann had done as early as 1854) divided the nautiloids into several major groups, which he subdivided according to the form of the conch, nature of the surface sculpture, shape of the septa, etc. Several of these groups have recently been studied in detail by Foerste, and it is the purpose of this paper to consider another, the Mixochoanites. This study was undertaken when during work on related forms the need for certain changes in nomenclature and arrangement of genera and families in this group became apparent.

PREVIOUS VIEWS IN REGARD TO THE CLASSIFICATION OF THE MIXOCHOANITES

The affinities of the little group of aberrant forms to which Hyatt eventually gave the name "Mixochoanites" have been a puzzle ever since their discovery by Barrande, who originally characterized them as being "très-bissares." He knew only a very few representatives, but he placed them in two or three genera and regarded them as constituting a family of equivalent rank with that which contained all the rest of the multitudinous nautiloids. He was followed in this by P. Fischer, but Zittel, Foord, Billings, Blake, Giebel, Wiltshire, and Wright apparently considered these forms much less distinct, and because of their short, stout living chambers placed them in the immediate vicinity of the gomphoceratoids. Koken placed them between the Orthoceratidae, in which he included *Gomphoceras*, *Endoceras*, and *Orthoceras*, and the Cyrtoceratidae, in which he included *Cyrtoceras* and *Phragmoceras*. Eichwald regarded *Ascoceras* as closely related to *Nothoceras* and the living *Sepia*; Roemer, however, placed it next to *Trochoceras*; Bronn and Woodward next to *Gyroceras*; Philippi between *Lituiles* and *Cyrtoceras*; and Nicholson in his sub-family Orthoceratidae. Lindström, who apparently studied the group in more detail than any of the other paleontologists except perhaps its discoverer, regarded it as related to the forms referred to *Cyrtoceras* by Barrande and to the poterioceratoids.

Hyatt in his *Genera of Fossil Cephalopods*, 1883, added genera hitherto not considered related to the group, and divided it into two families, the Mesoceratidae and the Ascoceratidae; *Mesoceras* Barrande and a then new genus *Billingsites* constituted the first, and *Aphragmites*, *Ascoceras*, *Glossoceras*, and *Ophidioceras*, all of Barrande, the second. These two families were placed between the Gomphoceratidae and the Maclonoceratidae in the suborder Elliphochoanoida, which included most of the nautiloids known at that time. However, in discussing the Mesoceratidae, Hyatt (p. 278) stated that they are "very distinct as a group from all other forms except the Ascoceratidae."

When he revised this classification in 1900, he emphasized this former opinion by placing these two families in a separate suborder,

the Mixochoanites, of equal rank with the Orthochoanites and Cyrtchoanites which received the remainder of the numerous forms previously grouped together as Ellipochoanoida. The content of the family Mesoceratidae was left unchanged, but *Ophidioceras*, which had been removed from the Ascoceratidae and made the type of a new family (Hyatt, 1893, p. 513) was placed in a different suborder, and *Choanoceras* Lindström and *Volborthella* Schmidt—genera which were unknown at the time the former classification was proposed—were added.

Since that time comparatively little progress has been made toward a better understanding of the group, and the nautiloids as a whole have been given very little attention in Europe. Broili has followed Zittel and left the Ascoceratidae as a single family placed next to the Orthoceratidae, and Pompeckj considered these forms an aberrant side-branch of that family. Dacqué regards *Ascoceras* as an aberrant offshoot of a group of nautiloids characterized by the possession of a slender tubular siphuncle throughout their development and typified by *Orthoceras*, *Cyrtoceras*, and *Nautilus*, but beginning with *Volborthella*. Föerster has given the mixochoanitic cephalopods as a group comparatively little attention, but he has pointed out that *Volborthella* should not be associated with them, has contributed much information in regard to *Billingsites* and *Ascoceras*, and has defined two additional genera, *Probillingsites* and *Shamattawaceras*.

Before attempting to evaluate any of these various schemes of classification, it will be well to review each of the genera concerned, and to define additional ones. For the sake of convenience, those that can be eliminated from the group most readily will be considered first.

Genus VOLBORTHELLA Schmidt 1884

Plate I, Figs. 1-14

About 1860 Dr. A. Volborth discovered minute conical gregarious fossils, which he believed to be cephalopods, in the Lower Cambrian blue shales near Tallinn (Revel), Estonia. These were exhibited at the Kaiserlichen Mineralogischen Gesellschaft, but they attracted no particular attention, and a notice of them was not published until 1881, when Fr. Schmidt briefly mentioned them and, following Volborth, referred them to "*Orthoceras*." Further study, however, caused him to doubt the validity of this reference, and in

1888 he published a more extensive description and additional illustrations of them and stated that although he could not present evidence positively eliminating them from the genus *Orthoceras*, he believed that their extreme smallness and thin shell, which failed of preservation when that of other fossils did not, justified a generic distinction, and he proposed to call them *Volborthella*, stating (p. 5) that he chose a name analogous with *Salterella*.

Since that time his species, *Volborthella tenuis*, the only described species of the genus, has been recognized in the Lower Cambrian at other localities near Tallinn, at Krasnoje Selo in the vicinity of Leningrad, at Lugnås in Wästergötland, in the Mjøsen region in Norway, and in Poland. Also, Matthew has referred specimens from the Lower Cambrian (and possibly the lowermost Middle Cambrian) of southern New Brunswick to this species. Unfortunately he did not describe his own material, but instead published a translation of Schmidt's description and added very few remarks in regard to the American specimens. His figures—pen sketches—also leave much to be desired, but as has already been suggested by Schindewolf (p. 70), it is extremely doubtful if the specimens studied by him are conspecific with the older European ones, and because of the shape of their sutures, the writer doubts that they are even congeneric.

The external characters of *Volborthella tenuis* have been described by Schmidt, Karpinsky, Bråstad, and Kiaer, and the internal structure by Karpinsky and Schindewolf. It will suffice here to state that the conch is very small (apparently never more than $3\frac{1}{2}$ mm. in diameter and 10 mm. long, and generally less than half that size), symmetrically cone-shaped, and camerated. The septa are moderately closely spaced and are depressed-cone-shaped; they bear a small central perforation which indicates the former presence of a narrow, tubular, vascular prolongation of the visceral region, presumably comparable to that which occupies the siphuncle of the living *Nautilus*. Schindewolf has observed structures that he interpreted as short straight septal necks, but the presence of connecting rings is entirely conjectural. Karpinsky has shown that the adoral part of the conch is strongly compressed laterally and the greatly restricted aperture is irregularly elliptical or slit-like. Very little direct information is available in regard to the composition of the shell as specimens retaining even fragments of it have not been observed, but the fact that in some of the ap-

parently uncrushed specimens (internal molds) the aperture appears to have been entirely closed led Karpinsky to the conclusion that the adoral part of the conch was soft and flexible whereas the rest was rigid. Schindewolf has discussed the composition of the shell at some length and has ably presented the available evidence for believing that the shell was calcareous rather than chitinous.

The relationship of this Lower Cambrian genus to the later cephalopods has recently become a moot question, and at present there is little agreement of opinion as to its proper place in our scheme of classification of the invertebrates. In 1900 Hyatt disregarded the prevalent opinion that its affinities were with the Orthoceratidae and placed it in the Ascoceratidae next to *Glossoceras*, apparently only because Schmidt's figures led him to the erroneous conclusion that its living chamber is "flaring and uncontracted" and because its septa are superficially similar to those of *Choanoceras*. It is now known that all but the extreme adapertural part of the living chamber is expanded adorally at the same rate as the phragmacone, and the aperture is greatly restricted; therefore, as recent authors have unanimously agreed, there seems to be no justification whatever for leaving this genus in the Mixochoanites.

Grabau and Shimer in 1910 created the suborder Protochoanites for the reception of this Cambrian genus, and in 1919 the senior of those two authors suggested that it was "ancestral, on the one hand, to the Holochoanites, and on the other to the Orthochoanites. By a crowding of the septa the endocones of the so-called siphuncle of the Holochoanites is produced, while a shallowing and separation of the septa produces the septa of the Orthochoanites. The septa chambers of the Holochoanites are a new feature. The endocones of the Holochoanites are considered the homologues of the septa of the Orthochoanites. On this view, the 'siphuncle' of the Holochoanites is the homologue of the entire Orthocern shell, while the endosiphuncle is the homologue of the Orthoceran siphuncle, and the endosiphonoling, when present, the homologue of the Orthocern shell proper."

Grabau has since (1922) reiterated these views, amplified his discussion of them, and added (p. 62) that the "*Cyrtochoanites* . . . may have been derived from primitive *Orthochoanites*, or they may represent an independent line of evolution from the ancestral stock . . ., the former view the more likely one."

^a

^a Since these statements were written, a still later discussion of this subject by

Similar conclusions were reached apparently independently by Dacqué in 1921, but he places *Volborthella* and *Orthoceras* in the same group, believing that the only distinction between them lies in the composition of the conch, probably conchyolin in the former but calcium carbonate in the latter; and he regards the large actinoceratoid siphuncle as well as that of the endoceratoids as the homologue of the conch of *Volborthella*, *Orthoceras*, *Cyrtoceras*, and *Nautilus*. He also postulates that whereas most of the later coiled nautiloids developed directly from *Volborthella* through *Orthoceras*, part of them have evolved from the endoceratoids by a reduction of the size of the siphuncle.

Abel has considered these views favorably, but Schuchert, Clarke, and Ulrich¹ questioned the validity of the homologies suggested by Grabau immediately after their postulation. Troedsson (pp. 16-20) has shown reasons for believing that *Volborthella* is not the direct progenitor of *Orthoceras* and that the siphuncle of *Orthoceras* is not homologically different from that of *Endoceras*, but he has accepted the conclusion that the conch of *Volborthella* is homologous with the siphuncle of the endoceratoids. Schindewolf (pp. 74-77) on the contrary regards *Volborthella* as a typical representative of the Orthochoanites, and has demonstrated that its conch as well as those of the later Orthochoanites is to be homologized with the entire conch of the endoceratoids and not with the siphuncle alone.

Foerste (1925, p. 4) has stated that "*Volborthella* has no relationship to this group [the Mixochoanites], but should be associated with *Salterella*." Schindewolf interpreted this statement as meaning that Foerste believes *Volborthella* not to be a cephalopod, as do Krause and Gürich². Foerste in all probability holds that opinion, but in 1924 Thomas Clark referred *Salterella* to the family Orthoceratidae and briefly presented his reasons for doing so, and more recently (1927) Poulsen, while studying forms from

Grabau (Bull. Geol. Soc. China, vol. 8, 1929, pp. 115-123) has come to the writer's attention. In it Grabau modifies his earlier conclusions in that both *Volborthella* and *Salterella* are regarded as primitive orthochoanites but are not believed to be ancestral to the holochaoanites, which are stated to have arisen from *Teihardoceras*, a hypothetical "genus." However, Grabau concludes this discussion with the following sentence: "These statements [presumably the whole paper], however, must be taken as mere suggestions and guides to future study which may or may not substantiate their validity."

¹ See "Discussion" following Grabau's paper of 1919.

² See "Diskussion" following Schindewolf's paper of 1928.

the Lower Cambrian of northwestern Greenland and comparing them with American specimens, has concluded that *Salterella*'s "cephalopod characters are very conspicuous." Clark's discussion is supplemented by a number of pen sketches that bear a striking resemblance to undoubted cephalopods, and he claims to have observed "siphonal collars" and a central aperture in each septum "from which a siphuncle-like tube projects backward to the next posterior septum." Specimens in the paleontological collections of Peabody Museum, Yale University, fail to show such structures, but in fairness it should be emphasized that they came from a different locality than those figured by Clark; however, Poulsen also was unable to observe "siphonal collars" and he states that "the shell of this genus differs from that of the later Nautiloidea in its structure."

It should also be mentioned in this connection that Walcott has recently (1913) described as "*Cyrtoceras cambria*" minute curved conical fossils from the Upper Cambrian of China that appear to possess saucer-shaped septa and a small marginal siphuncle, the structure of which, unfortunately, was not investigated. These fossils undoubtedly represent a new and distinct genus, and the published figures of them certainly bear out their postulated cephalopod affinity. However, it will be well to reserve judgment as to their significance and relationships until the structure of their siphuncle has been investigated and they have been studied by more than one observer. It should perhaps be mentioned that Kobayashi (1931) has recently suggested that "*Cyrtoceras cambrica* . . . may possibly be an Ellesmereoceroid, as judged from its description and illustrations," whereas Schindewolf (1928, p. 81) is inclined to regard it as a cyrtchoanite and points out that its narrow siphuncle indicates that it is not a holochanite.

With the exception of this single minute form, which is imperfectly known, even questionable cephalopod remains appear to be entirely absent from all of the Middle Cambrian (except possibly its very base) and all of the Upper Cambrian^{2a} (Ozarkian excluded); and Foerste (1925, p. 14) has recently shown that all of the Ozarkian and Canadian cephalopods are holochanites. Those who postulate that either or both of the Lower Cambrian

^{2a} Grabau (Bull. Geol. Soc. China, vol. 8, 1929, p. 122) has recently stated that orthoceracones and cyrtoceracones which appear to have orthochaoanitic siphuncles occur in the "uppermost Cambrian beds" of Shantung. However, no description or illustration of these forms has so far been published.

forms, *Volborthella* and *Salterella*, are cephalopods are almost unanimous in the conclusion that they are orthochoanites; therefore, if we are to regard them as ancestral to the later cephalopods, we must postulate that orthochoanites, which for some unexplained reason failed to leave a record in Middle and Upper Cambrian times, evolved into holochoanites, which, in turn, later gave rise to orthochoanites; or that orthochoanites actually existed during Middle Cambrian, Upper Cambrian, Ozarkian, and Canadian times, but we have failed to discover a trace of them as yet. Both of these possibilities are extremely improbable, and it now seems to the writer that we should regard *Volborthella* and *Salterella*, which apparently should be associated in our classification, as pteropods, conulariads, or foraminifers, i.e., not cephalopods; or, if they are cephalopods, we should consider them as representing an aberrant side-branch which learned to secrete "hard-parts" early in Cambrian times but died out³ before or shortly after the beginning of the Middle Cambrian, whereas the forms that were ancestral to the rest of the cephalopods remained naked and therefore recordless until Ozarkian times.

Genus OPHIOCERAS Barrande 1865

[= *Ophidioceras* Barrande 1867, but not *Ophioceras* Hyatt 1867]

Plate II, Figs. 1, 2

The generic term "*Ophioceras*" was originally introduced⁴ in 1865 by Barrande in a volume of plates (explanation of plate 45) as a subgenus of *Lituites* to include the forms in which the free straight anterior portion of the conch is short and the aperture contracted, or, to be exact, "pour les formes à crosse courte et à ouverture contractée, qui caractérisent la faune troisième silurienne et qui contrastent avec les *Lituites* à longue crosse et à ouverture non contractée? de la faune seconde." The text to accompany these plates did not appear until two years later, and in it Barrande (p. 174) transformed his term *Ophioceras* to *Ophidioceras*, stating that he did so to avoid confusion with

³ The specimens from the Stones River of Tennessee that were briefly described by Safford (Geology of Tennessee, p. 289, Nashville, 1869) as "*Salterella Billingsi*" need to be restudied, but there seems to be little justification for their reference to the Lower Cambrian genus *Salterella*.

⁴ "*Ophioceras*" *simplex* was figured by Barrande as early as 1855 (Bull. Soc. géol. France, 2e sér., t. 12, pl. 5, fig. 6) but was referred to *Lituites*.

*Ophiceras*⁵, which was applied by Suess⁶ to a group of ammonites during the printing of the plates and before their publication. According to the International Rules of Zoological Nomenclature (Recommendations following Article 36) *Ophioceras* is not to be rejected as a homonym of *Ophiceras*; therefore Barrande's earlier term, having priority, must be regarded as the valid name of the genus.

In 1867 Hyatt⁷, without taking into consideration Barrande's earlier use of the term, employed *Ophioceras* for a then new genus of ammonites. Later, in 1900 (p. 575) he listed this genus as a synonym of one of his later genera *Caloceras*⁸ Hyatt 1871, apparently rejecting his earlier term as a synonym of *Ophioceras* Barrande 1865, but not stating so. Nevertheless, *Ophioceras* Hyatt was inadvertently resurrected in the second edition of the Zittel-Eastman *Text-book of Paleontology* (p. 655) by J. P. Smith and *Caloceras* was dropped. Broili (1924, pp. 571, 572) places these two genera in different subfamilies, but as far as the writer has been able to learn, they are synonyms and *Caloceras* is in good standing whereas *Ophioceras* Hyatt is to be rejected as a homonym of *Ophioceras* Barrande.

Barrande did not designate a type for his subgenus *Ophioceras* [*Ophidioceras*], and recently Foerste (1930, p. 19) has selected "*Ophidioceras simplex* Barrande" as such. However, as early as 1868, Tate⁹ listed *Lituites nakhholmensis* Kjerulf of the Ordovician of Nakholmen, Norway, as the genotype, and this designation is

⁵ This term is now generally ascribed to Greisbach, who however did not use it until 1880 (Records of the Geol. Survey of India, vol. 13, p. 109). Since it was preoccupied, a new generic term is needed for Greisbach's genus, and it is here proposed to call it *Greisbachoceras*, in honor of its original describer. The type of this genus is *Greisbachoceras* [*Ophiceras*] *tibeticum* (Greisbach) of the Lower Triassic of the Himalayas, and the generic characters are ably set forth by Greisbach (op. cit.), Hyatt and Smith (U. S. Geol. Survey Professional Paper 40, pp. 117-118, 1905), and Krafft and Diener (India Geol. Survey Mem., ser. 15, vol. 6, mem. 1, pp. 80-81, 1909).

⁶ Suess, Eduard, Anzeiger der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe, II. Jahrgang, p. 112, 1865.

⁷ Hyatt, Alpheus, The fossil cephalopods of the Museum of Comparative Zoölogy: Harvard Coll. Mus. Comp. Zoöl. Bull., vol. 1, p. 75, 1867.

⁸ Proposed in a footnote by Alpheus Hyatt (On reversions among the ammonites: Boston Soc. Nat. Hist. Proc., vol. 14, p. 29, 1871), and later treated of at length by the same author (Genesis of the Arietidae: Memoires Museum of Comparative Zoölogy at Harvard College, vol. 16, no. 3, pp. 136-154, 1889).

⁹ Tate, Ralph, Appendix to the Manual of Mollusca . . . by S. P. Woodward, 2d ed., p. 8, London, 1868.

“not subject to change.” This latter species is not very similar to the forms figured and described by Barrande, which came from the Middle Silurian of Bohemia, and as it is rather deeply involute, though becoming less so near the aperture, and does not possess a free straight extension of the living chamber, it is not congeneric with them. Nevertheless, it was considered so by Barrande, and although the designation of it as the genotype seems very inappropriate, it is “not subject to change.”

Kjerulf¹⁰ figured this species and listed the general horizon and locality from which the type came, but he did not describe it. No other forms are known to the writer that are congeneric with this species, and a generic diagnosis is not attempted here as neither specimens nor description is available for study; Kjerulf's figures, however, are reproduced.

In his *Genera of Fossil Cephalopods*, 1883 (p. 279), Hyatt placed *Ophidioceras* Barrande [= *Ophioceras* Barrande] in the family Ascoceratidae, and stated: “The costated, compressed whorls have some resemblance to those of *Ascoceras* and the aperture is closely similar to *Glossoceras*. . . . We place them [the *Ophidioceras* shells] provisionally near *Ascoceras* on account of the Y shaped apertures and form of whorl and costations.” However, by 1893, Hyatt had become aware of the incorrectness of this reference, and he (p. 513) removed the genus in question from the Ascoceratidae and made it the type of a new family, which in 1900 (p. 520) he placed in a different suborder from that to which he referred *Ascoceras* and its allies. This latter classification is by far the more tenable, and it will suffice here to state that none of the forms that have been referred to “*Ophidioceras*” appears to be at all closely related to any of the mixochoanitic nautiloids.

Genus EUOPHIOCERAS Miller, n. gen.

Plate II. Figs. 3-7

As noted above Barrande established the genus *Ophioceras* [= *Ophidioceras*] for a group of Silurian forms from Bohemia but included an Ordovician form from Norway, apparently only because of a superficial resemblance of the aperture. Unfortunately, this Ordovician form was later chosen as the genotype, and as

¹⁰ Kjerulf, Theodor, Veiviser ved Geologiske Excursioner i Christiania Omegn, . . . , p. 9, text fig. 21, p. 13, Christiania, 1865.

it is not congeneric with the Silurian ones, a new generic name is needed for the latter. In as much as the genus was actually established for the Silurian forms, the term *Euophioceras* is here proposed for them, and *Lituities* [*Ophioceras*, *Ophidioceras*] *simplex* Barrande of Stage E of the Middle Silurian of Bohemia is designated as the genotype.

The characters of this genus are admirably set forth by Barrande (pp. 174-176), and the reader is referred to his voluminous monograph for a detailed generic diagnosis; also a concise diagnosis has recently been published by Foerste (1930, pp. 19-20). The following species should be referred to this genus: *Ophidioceras* [*Ophioceras*] *amissus* Barrande, *O. proximus* Barrande, *O. rudens* Barrande, *O. simplex* (Barrande), *O. tener* Barrande, *O. tessellatus* Barrande, all of Stage E of the Silurian of Bohemia; *O. reticulatum* Angelin and *O. rota* Lindström of the Middle Silurian of Gotland; *Lituities articulatus* Sowerby¹¹ and *Ophidioceras geometricum* Blake of the Silurian of England; *Ophidioceras wilmingtontense* Foerste of the Cedarville dolomite of Ohio and the Racine dolomite of Wisconsin; *O. welleri* Foerste of the Racine of Illinois; and probably the specimen from the Silurian of Cornwallis Island, Arctic America, that was described by Salter¹² as "*Lituities* —, n. sp."

Barrande (vol. 2, texte 4, p. 510) included *Lituities nakholmensis* Kjerulf of the Ordovician of Nakholmen, Norway, and *Clymenia depressa* (Eichwald) 1860 [= *Nautilus depressus* Eichwald 1840] of the Middle Ordovician of Odinsholm, Estonia, in the same genus as all of the above listed forms known at that time, but the internal molds of both of those species are smooth and the adoral part of their conchs is in contact with the preceding volution. It is true that the degree of involution in both species decreases adorally and "*Nautilus*" *depressus* may belong in the same family as *Euophioceras*, but the general shape of the conch and the nature of the sutures of *Lituities* [*Ophioceras*] *nakholmensis* is so different from that of the species here referred to

¹¹ Sowerby, James de C., in Murchison, R. I., *The Silurian System* . . . , part 2, p. 622, pl. 11, fig. 5 [but not fig. 7, the original of which was later described as "*Cyrtoceras extricatum*" by Blake (A monograph of the British fossil Cephalopoda, pt. 1, pp. 183-184, 1882)], London, 1839.

¹² Salter, J. W., *Geology*; Appendix in Sutherland, Peter C., *Journal of a voyage in Baffin's Bay and Barrow Straits* . . . , vol. 2, p. ccxxii, London, 1852.

Euophioceras, that it seems very doubtful if they are at all closely related.

To avoid ambiguity, it should perhaps be repeated here that none of the above listed forms is at all closely related to any of the mixochoanitic cephalopods, and *Euophioceras* should be associated with *Lituiles* and not the ascoceratoids.

Genus *MESOCERAS* Barrande 1877

Plate II, Figs. 8-12

This genus was established by Barrande in 1877 (pp. 198-200) on a single internal mold of a living chamber from Stage E of the Middle Silurian of Bohemia. Barrande states that he kept the specimen for twenty-five years before describing it, waiting in vain for the discovery of other specimens that would elucidate more of the specific and generic characters, and since that time no other representative of the genus has been found.

The holotype of the only known species, *Mesoceras bohemicum* Barrande, appears to represent a short, stout brevicone, that is elliptical in cross section as it is slightly depressed dorso-ventrally. The living chamber is very short and the aperture is greatly restricted dorsally and somewhat so ventrally, but not at all laterally. It is narrowly elliptical in outline, but there appears to be a small hyponomic sinus on the ventral side. Barrande states that as the specimen is preserved in black slate he was not able to determine definitely whether the ventral notch was original or was due to an accident during preservation, but the growth lines bend adapically as they cross an indistinct longitudinal median groove on the ventral side of the conch and therefore indicate that the notch represents a hyponomic sinus. The sutures are simple and straight and are directly transverse to the long axis of the conch. The siphuncle is central in position and is relatively small at its passage through a septum, but the shape of its segments and its general nature are not known; nor is anything known as to the nature of the phragmacone.

Barrande was unable to place this genus satisfactorily in his classification, for he divided the nautiloids into two major groups on the basis of the nature of the aperture, and he considered that of *Mesoceras* as neither simple nor composite. Hyatt in 1883 (p. 278) made this genus the type of a new family and associated his own then new genus *Billingsites* with it, apparently only because

both were brevicones with short, bulbous living chambers and restricted apertures. He placed this family between the Gomphoceratidae and the Ascoceratidae but stated that the members of it were "very distinct as a group from all forms except the Ascoceratidae." Later, in 1900 (pp. 515-516) he combined this family with the Ascoceratidae to form a new suborder, the Mixochoanites. Zittel and Broili followed Hyatt in part and left *Mesoceras* associated with *Billingsites*, but Fischer, Foord, and Lindström placed it with the gomphoceratoids. This latter classification seems logical to the writer, but until the nature of the siphuncle is established, it will not be possible to classify the genus with certainty. However, it does not appear to be at all closely related to any of the true Mixochoanites, i.e., *Ascoceras* and its allies, and there seems to be no justification for leaving it in that suborder.

Genus *PROBILLINGSITES* Foerste 1928

Plate III, Figs. 10-13

Foerste (1928, pp. 317-320) has recently recognized that four of the species previously referred to *Billingsites* are distinctly more primitive than typical representatives of that genus and has proposed the generic term *Probillingsites* for them. Unfortunately, each of these species is based on a single fragmentary specimen, the earlier stages of the conch are not known, and the siphuncle has not been observed. Nevertheless, it seems clear that this group is distinctly intermediate between *Billingsites* and its progenitor, an *Oncoceras*-like form, and it should be regarded as the most primitive member of the Mixochoanites.

The genus includes *Probillingsites welleri* Foerste probably from the Galena of Wisconsin, *P. williamsportensis* (Foerste) from the Catheys formation of western Tennessee, *P. primus* (Fritz)¹³ of the Upper Cobourg member of the Utica group of southern Ontario, and *P. manitoulinensis* (Foerste) from the Meaford member of the lower Richmond of Manitoulin Island. The last species listed is of Upper Ordovician age and the two preceding ones are of Middle Ordovician; the horizon of the other species, the genotype, is uncertain, but there is good reason to believe that it also is Middle Ordovician in age. The genus then appears to be characteristic of the Middle Ordovician but to have

¹³ Described in Parks, W. A., Faunas and stratigraphy of the Ordovician black shales and related rocks in southern Ontario: Royal Soc. Canada Trans., 3d ser., vol. 22, pp. 85-86, 1928.

continued on into the Upper Ordovician, where its place is largely taken by *Billingsites* and *Schuchertoceras*, discussed below.

The conch is breviconic and moderately small, and in complete specimens would probably be similar in shape to that of *Onco-ceras*, but only the adoral obese, ovoid expansion is known. This consists of the living chamber and the two to four adoral camerae. It is typically depressed dorso-ventrally, but in *P. manitoulinensis*, the last representative of the genus known, it is slightly compressed laterally. The dorsum is straight or slightly concave or convex, but the venter is invariably strongly convex, with the result that the specimens appear very obese. The maximum transverse dimensions of this ovoid expansion are attained near its mid-length, and the conch contracts both adapically and adorally from that point. There is a short indistinct neck-like extension of the living chamber next to the aperture, called the "neck" by Foerste, but the exact nature of the aperture has not been determined. The adoral septa, the only ones known, are not transverse to the long axis of the conch, as are those of most nautiloids, but are strongly inclined to it, and along the lateral sides of the conch the sutures slope strongly adorally from the venter and cross the dorsum as broad rounded saddles; the dorsal part of the living chamber is therefore very much shorter than the obese ventral part. The sutures are slightly sigmoidal, but there is no strong reversal in their curvature, and the dorsal saddles of the adoral septa do not extend as far orad as they do in *Billingsites*.

The sutures of *P. primus* and *P. manitoulinensis* are distinctly intermediate between those of *P. williamsportensis* and *P. welleri* and those of *Billingsites*; they are more closely crowded than those of the last two mentioned species, more strongly inclined to the long axis of the conch, and more strongly sigmoidal, and at least two of them appear to coalesce along the lateral sides of the conch. Also the conchs of both of these species are distinctly concave along the dorsum near the junction of the phragmacone and the living chamber, and the adoral neck-like extension of the living chamber is longer and much more distinct than it is in the other two representatives of the genus. In view of these differences, and since these two species occur in a higher horizon than does the genotype and *P. williamsportensis*, it may eventually prove desirable to recognize them as representing a distinct genus interme-

diate between *Probillingsites* and *Billingsites*, but at present such a generic refinement seems unnecessary.

Most of the paleontologists who have studied *Ascoceras* and its allies have agreed that the conch was truncated during the life of the individual, i.e., the earlier stages of the phragmacone were broken off along a septum and abandoned after maturity was reached. This inference is based largely on the fact that with very few exceptions only the extreme adoral part of the phragmacone has been found attached to the living chamber—the genus *Ascoceras* was known for a decade before the younger stages of the phragmacone were discovered. Similarly, truncation can be inferred in *Probillingsites*, the earliest and most primitive member of the group known, for none of the described representatives of the genus retains the adapical part of the phragmacone, and all appear to have been bounded adapically by a moderately large, well developed septum, the septum of truncation.

Genus SHAMATTAWACERAS Foerste and Savage 1927

Plate III, Figs. 1-3

Very little information is available in regard to the genus *Shamattawaceras*, for it is based on a single rather poorly preserved, fragmentary specimen. Externally, at least, it is very similar to *Probillingsites*, and in view of no evidence to the contrary, it should be associated tentatively with that genus in our scheme or classification and accordingly referred to the Mixochoanites.

The holotype of *Shamattawaceras ascoceroides* Foerste and Savage, the only known representative of the genus, came from the Shamattawa limestone (Richmond) of northeastern Manitoba, southwest of Hudson Bay. It is an internal mold representing much of the living chamber and the adoral three camerae, i.e., the adoral obese portion of the conch. It is not complete aperturally, and it is bounded adapically by the impression of a large well developed septum; the earlier stages of the phragmacone may have been truncated during the life of the individual as they were in most of the Mixochoanites.

The known portion of the conch is almost semicylindrical in shape but is slightly curved lengthwise; it is almost semicircular in cross section as it is greatly flattened ventrally, narrowly rounded ventro-laterally, and evenly rounded dorso-laterally and dorsally. The venter is convex lengthwise, and the dorsum appears to be slightly so. The adapical part of the holotype is expanded

orad very gradually, but the rate decreases adorally and the adoral part of the specimen, which does not represent the aperture is neither contracted nor expanded in a lateral direction. The maximum dorso-ventral diameter of the conch apparently is attained near the mid-length of the specimen, and it decreases both apicad and orad of that point. The specimen is bounded adapically by the impression of a septum which was only very slightly convex apicad in a lateral direction but rather strongly so in a dorso-ventral direction as its dorsal half was curved strongly orad. Since the lateral and apical sides of the specimen are only very slightly convex, it appears subquadrate when viewed from above or below, i.e., in dorsal or ventral aspect, and it would appear so in longitudinal section. Unfortunately, nothing is known as to the nature of the adoral part of the living chamber or the aperture.

On the flat ventral side of the holotype all four of the sutures are parallel and very close together, and they are almost transverse to the long axis of the conch but curve very slightly apicad and therefore form very broad shallow ventral lobes. Along the lateral sides of the specimen they diverge gradually and curve orad at successively greater angles. They form broad, deep rounded saddles as they cross the dorsum, and the dorsal part of the living chamber is therefore very much shorter than the ventral part. Nothing is known in regard to the siphuncle of this genus as no trace of it remains in the only representative that has so far been found.

Although many of the most significant of the generic characters of this form are not known, e.g., the adoral and adapical portions of the conch, the siphuncle, and the aperture, the general shape of the preserved part of the conch and the nature of the sutures indicate a relationship with *Probillingsites*, and in view of complete lack of evidence to the contrary, this genus, for the present, at least, should be associated with *Probillingsites* and placed in the Mixochoanites. As far as is known at present, it differs from *Probillingsites* chiefly in the shape of the adoral obese expansion of the conch; that of *Probillingsites* is subovoid in form and broadly elliptical in cross section, whereas that of the genus under consideration is almost semicylindrical in shape and semicircular in cross section. Occurring as it does in the Richmond, this genus may have developed out of *Probillingsites* or its progenitor, or it

may represent a parallel development of an unrelated stock; the nature of the siphuncle and the aperture, when fully known, will doubtlessly remove this uncertainty and enable us to classify the genus definitely.

GENUS *BILLINGSITES* Hyatt 1883

Plate IV, Figs. 1-6

Ascoceras-like forms were reported from the Ordovician (English Head of Anticosti Island) as early as 1857 by Billings, but it was not recognized that they were generically distinct from typical *Ascoceras* until 1883¹⁴. In that year Hyatt (p. 278) proposed the generic term *Billingsites* (inadvertently written "*Billingoceras*", p. 279) for them, designated *Ascoceras canadense* Billings as the type, and defined the genus as including "Silurian species having stout cones, almost globular on account of their truncation and which have dumb-bell shaped apertures, without ventral sinuses." Later, in 1900 (p. 516) he redefined the genus as follows: "Aperture without hyponomic sinus. Gerontic living chamber partly filled by dorsal sigmoidal saddles as in *Ascoceras*, but septa complete on ventral side. Silurian."

Neither of these definitions is very lucid and both are erroneous, for no known representative of the genus possesses a dumb-bell shaped aperture, and the latter definition implies that the septa are not complete on the ventral side of *Ascoceras*, a view held by Barrande but previously recognized by Hyatt (1883, pp. 278-279) as incorrect. Therefore, the genus, though recognized by Zittel and Bassler, was almost entirely neglected until 1924, when it was revived by Foerste and placed on a firm basis. Since that time it has been recognized by various authors, and a considerable number of species has been referred to it.

The type species, *Billingsites* [*Ascoceras*] *canadensis* (Billings) of the English Head and Vauréal (Richmond) of Anticosti Island has recently been studied by Foerste, and the holotype has been redescribed and figured. It should be emphasized that only the adoral obese, ovoid expansion of the conch is known; the earlier stages of the phragmacone apparently were truncated during the

¹⁴ As early as 1867, Barrande (p. 353) stated that "*Ascoceras*" *deforme* Eichwald of the Upper Ordovician (or Lower Silurian) of Estonia "n'est pas un *Ascoceras*" but reminds of *Gomphoceras*; this conclusion, however, was reached largely because of the inadequacy of Eichwald's figure and description.

life of the individual, and all the knowledge we have of them in this genus is inferred from the scar or cicatrix of attachment.

The known portion of the conch of the genotype, the adoral ovoid expansion, consists of the living chamber and the adoral three cameracae. It is subovate in shape, narrowly rounded apicad, and somewhat contracted orad; its maximum transverse dimensions are attained near its mid-length, and it is elliptical in cross section as it is slightly depressed dorso-ventrally. The adoral end of the living chamber is projected into a short indistinct neck-like extension which is contracted orad only very slightly, and the aperture is broadly elliptical in outline. Nothing is known in regard to the exterior of the shell of this species¹⁵, but the internal mold is smooth, with the exception of a broad, shallow, indistinct transverse constriction on the apical fourth of the specimens.

The impression of the septum of truncation on the internal mold shows that it is moderately convex apicad, circular (or nearly so) in outline, asymmetrically subconical in shape, and strongly oblique to the long axis of the conch; it slopes orad from the venter. The suture of the next septum is essentially parallel and almost in contact with the septum of truncation along the ventral and lateral sides of the conch, but along the dorso-lateral sides it curves abruptly ventrad and orad and continues in that direction to the middle of the lateral sides of the conch, where it gradually ceases to swing ventrad and then curves rather abruptly dorsad and continues across the dorso-lateral and dorsal sides of the conch as an essentially straight line transverse to the long axis of the conch. The next septum is almost parallel to the preceding one; along the venter these two septa are about 2 mm. apart, but they gradually converge dorsally, and on the dorso-lateral sides of the conch, where the strong reversal in their curvature occurs, they are only a little more than $\frac{1}{2}$ mm. apart. Orad of this point they gradually diverge so that they are some 9 mm. apart along the dorsum. The ventral trace of the adoral suture can not be made out on the specimen available for study, and Foerste shows only two sutures crossing the venter of the holotype; nevertheless,

¹⁵ Very little information is available in regard to the shell of any of the known representatives of this genus, but it should be mentioned that that of *Billingites costulatus* (Whiteaves) bears both transverse bands and small transverse ridges, but the internal mold of its conch is smooth; the thickness of the shell in that species varies from $\frac{1}{4}$ - $\frac{1}{2}$ mm. along the dorsum to nearly 1 mm. along the venter.

it seems probable that the adoral suture is essentially parallel to the preceding one along the venter and then coalesces with it along the ventro-lateral part of the conch. These two separate just orad of the strong reversal in their curvature on the dorso-lateral part of the conch, and as they gradually diverge orad, they are 3.5 mm. apart along the dorsum.

A median longitudinal section shows that the ventral two-thirds of the first (oldest) of these three adoral septa is almost straight (very slightly convex apicad), but the dorsal third is bent abruptly orad so as to form a broad shallow camera along slightly more than half of the dorsal part of the living chamber. The next septum is almost parallel to the first and throughout much of its length is almost in contact with it, but the two diverge slightly in the ad-apical end of the specimen and rather strongly in the adoral half of it. The adoral septum is almost parallel with the preceding one, but it coalesces with that septum a short distance (some 5 mm.) dorsad of the septal necks and then separates from it some 10 mm. in advance of there; the two diverge orad very gradually and are 3.5 mm. apart along the dorsum.

The nature of the siphuncle of the earlier stages of the phragmacone is not known, but that of the adoral ovoid portion of the conch is ventral in position and is moderately large; its segments are expanded so greatly within the camerae that they appear nummuloidal. The septal necks or funnels are very short and very strongly recurved; the connecting rings are parallel and almost in contact with the septa throughout most of their length. The siphuncle measures about 4 mm. in diameter at its passage through the septum of truncation and expands to a diameter of about 9 mm. within the adjacent camera; it expands orad only very gradually, but its opening into the living chamber is much larger than that in the preceding septum and measures about 7 mm. in diameter.

Recently a considerable number of species has been referred to this genus, but it seems to the writer that they are not all congeneric with the above described genotype. Foerste has separated one group of them and proposed the generic name *Probillingsites* for it, and another group is distinguished below under the name *Schuchertoceras*; the latter is typified by *Billingsites anticostiensis* (Billings) and is characterized by the possession of a so-called

"basal" septum between the septum of truncation and the strongly sigmoidal septa.

As near as can be told from the material available for study by the writer and the existing descriptions and figures, the following species possess the same general characters as *Billingsites canadensis*, the genotype of *Billingsites*, and should therefore be referred to that genus: *B. acutus* Foerste of the English Head (Richmond) of Anticosti Island, *B. elongatus* Foerste probably of the Ellis Bay (Gamachian) of Anticosti Island, *B. borealis* (Parks) of the Shamattawa (Richmond) of northeastern Manitoba southwest of Hudson Bay, *B. costulatus* (Whiteaves) of the Dog Head member of the Red River (Richmond) of southern Manitoba, *B. multicameratus* Miller and *B. bellicinctus* Miller of the Lander sandstone member of the Bighorn (Richmond) of west-central Wyoming, and *B. deformis* (Eichwald) of the Lyekholm (uppermost Ordovician or lowermost Silurian) of Dagö Island, Estonia.

Also, Foerste has mentioned in his recent publications that unnamed representatives of "*Billingsites*" occur in the Stony Mountain (upper Richmond) of southern Manitoba, the Ogonotz division of the Stonington (Richmond) of the peninsula east of Escanaba in northern Michigan, the base of the Whitewater (Richmond) of southwestern Ohio and adjacent parts of Indiana, the Maquoketa (Richmond) of northeastern Iowa, the Kallholm or Upper Lepstaena limestone (uppermost Ordovician or lowermost Silurian) at Dalbyn in the Dalarne area of central Sweden, and the Gastropod limestone (uppermost Ordovician or lowermost Silurian) of the Ringerike area southwest of Oslo, Norway; three species are known to be represented at the last locality listed. Part of these forms doubtlessly represent *Billingsites* s.s. and part the genus described below as *Schuchertloceras*, but the published information in regard to them is not sufficient to allot them.

In summary then it can be stated that *Billingsites* is widely distributed in North America and is represented in Estonia and doubtlessly in southern Scandinavia. It is confined to the Upper Ordovician (Richmond and Gamachian) in North America, but in northwestern Europe it probably occurs in the Lyekholm of Estonia and the Gastropod limestone of Norway, which are either uppermost Ordovician or basal Silurian; their age is at present a moot question. Apparently this genus developed out of *Probillingsites* after the close of the Middle Ordovician in an arctic or

subarctic sea, probably a branch of the northern Atlantic, and spread from there southward into North America and northwestern Europe during the latter part of the Upper Ordovician.

Billingsites differs from its progenitor, *Probillingsites*, in that its adoral sutures are much more complex; those of *P. primus* (Fritz), the most highly developed representative of *Probillingsites* known, are only slightly sigmoidal and there is no strong reversal in their curvature on the dorso-lateral walls of the conch as there is in *Billingsites*. The conch of *Shamattawaceras* is shaped differently, and its sutures are comparable in their complexity to those of *Probillingsites*. Comparisons with later derivatives of this stock are given below in the discussions of the genera concerned.

Genus SCHUCHERTOCERAS Miller, n. gen.

Plate III, Figs. 4-9

As mentioned above in the discussion of *Billingsites*, part of the species that have been referred to that genus are characterized by the possession of a so-called "basal" septum between the septum of truncation and the strongly sigmoidal adoral septa. These seem to constitute a natural group, and the generic name *Schuchertoceras*¹⁶ is here proposed for it and *Billingsites* [*Ascoceras*] *anticostiensis* (Billings) of the English Head and Vauréal (Richmond) and Ellis Bay (Gamachian) of Anticosti Island is designated as the genotype. It is true that the biological significance of this "basal" septum is not as yet fully understood, but since, as is shown below, its presence or absence can be used to distinguish two closely related groups that became distinct after the Middle Ordovician and underwent parallel evolution during the Late Ordovician and Middle Silurian, its taxonomic value is obvious. It should not be imagined that the basal septum can be explained merely by assuming truncation along a more posterior septum; its development was much more complicated than that, and specimens from which the "basal" camera has been broken away do not resemble representatives of *Billingsites*—their incompleteness is obvious. Furthermore, as far as is now known, the choice of the septum along which truncation occurred in the mixochoanitic cephalopods was not left to chance but was predetermined, and (with

¹⁶ Named in honor of Professor Charles Schuchert, who fomented and fostered much of the recent geological work in southeastern Canada, whence came most of the known representatives of this genus.

the possible exception of *Choanoceras*) the septum of truncation invariably marked the junction of the adolescent part of the conch, in which the siphuncle was orthochoanitic in structure, with the mature part, in which it was cyrtochoanitic.

The holotype of *Schuchertoceras anticostiense* was originally referred by Billings (1862, p. 164) to "*Ascoceras Newberryi*," but was later (1866, p. 60) recognized by him as representing a distinct species and given a specific name. Unfortunately it has since been lost. Foerste (1928, pp. 259-260) recently designated a neoholotype (Canada Geol. Survey, 2334a2), and although it does not appear to the writer to be very similar to the original type as sketched by Billings, it is here accepted as the type of the species and is designated as the type of the new genus.

Only the adoral obese expansion of the conch is known, and it is comparable in shape to that of *Billingsites* ss. but is somewhat shorter and less narrowly rounded apicad and is therefore less ovoid and more nearly globular in shape. As it is slightly depressed dorso-ventrally, it is broadly elliptical in cross section. The adoral neck-like extension of the living chamber is slightly more prominent than that of typical *Billingsites*, but the apertures of both are broadly elliptical in outline; their lateral diameters are distinctly longer than their dorso-ventral.

The scar or cicatrix of attachment of the earlier stages of the phragmacone to the known portion of the conch (i.e., the impression of the septum of truncation) is not preserved on most of the numerous specimens of the type species available for study, but on one of them (Yale Peabody Museum, 3807b), which is strikingly similar to the neoholotype, it is very distinct. It shows that the septum of truncation of that specimen was moderately convex apicad and was strongly inclined to the long axis of the conch; it sloped orad from the venter. The ventral half of the suture of that specimen is normal, i.e., broadly rounded, but near the center of the lateral sides of the conch the suture curves rather strongly dorsad and continues, almost transverse to the long axis of the conch, across the dorsum approximately midway between the apex of the specimen and the basal suture; the scar of the septum of truncation is therefore more strongly convex ventrally than dorsally and is subelliptical in outline. The next septum orad, the so-called basal septum is essentially circular in outline. Its suture is almost parallel to that of the preceding septum along the venter

but is slightly sigmoidal laterally, and the two sutures converge slightly on the ventro-lateral part of the conch and diverge markedly on the dorso-lateral; in the specimen under consideration they are about $3\frac{1}{2}$ mm. apart along the venter, $1\frac{1}{2}$ mm. near the center of the lateral sides, and $11\frac{1}{2}$ mm. along the dorsum. The suture of the next septum is close to that of the basal septum and almost parallel with it along the ventral half of the conch, but near the center of the lateral sides of the conch, it bends abruptly orad and ventrad and continues in that direction to the center of the ventro-lateral sides of the conch, where it gradually ceases to swing ventrad and then curves rather abruptly dorsad and continues across the dorsum as an essentially straight line approximately transverse to the long axis of the conch; it crosses the dorsum about 15 mm. orad of the point where the basal suture crosses it. The adoral suture is very close to the preceding suture along the venter and apparently coalesces with it along the ventro-lateral sides of the conch. The two separate again near the mid-point of the ventro-lateral part of the conch and continue across the dorsum as two essentially parallel lines relatively close together.

A longitudinal section through the siphuncle shows that the basal septum is only very slightly convex and is inclined to the long axis of the conch at some forty-five degrees. The next septum is only about 1 mm. from the preceding one along the venter, but it diverges slightly from it in the vicinity of the septal necks; immediately dorsad of the necks the two septa converge slightly until they are almost in contact and then diverge markedly as the septum under consideration gradually curves orad and, after swinging slightly ventrad, curves dorsad again to meet the dorsum far orad of the point where the preceding septum meets it. The adoral septum is not well preserved in the ventral part of the sections available for study, but it appears to coalesce with the preceding septum slightly ventrad of the siphuncle, and it separates from it only in the extreme dorsal part of the conch, some 5-10 mm. below the dorsum. Foerste has recently (1928) figured a specimen that shows three septa orad of the basal septum and referred it to this species, but the shape of its conch as well as its sutures is so different from that of the neoholotype that the writer doubts that they are conspecific.

The earlier stages of the phragmacone and the siphuncle of this genus are not known, but in the known portion of the conch of the

genotype the siphuncle is ventral in position and is relatively small at its passage through a septum but is expanded transversely within the camerae; the septal necks are short and strongly recurved. The connecting ring between the septum of truncation and the basal septum is moderately expanded transversely between the septa, but it is constricted centrally which suggests that during the development of the individual a septum that was later resorbed was formed midway between these two septa. The next and most adoral segment of the siphuncle is much more strongly expanded within the camera and is not constricted centrally.

As near as can be told from the material available for study and the published descriptions and figures, which refer almost exclusively to external features, the following species possess the same general characters as the above described genotype and should therefore be referred to *Schuchertoceras*: *Billingsites* [*Ascoceras*] *newberryi* (Billings)¹⁷ of the English Head (Richmond) of Anticosti Island; *Billingsites logani* Cooper of the Upper Ordovician of the eastern part of Gaspé Peninsula, Quebec; *Billingsites broadsoni* Foerste of the Kallholn or Upper Leptaena limestone (uppermost Ordovician or lowermost Silurian) of the Dalarne area northwest of Stockholm, Sweden; and *Ascoceras norvegicum* Barande or southeastern Norway, presumably from the Gastropod limestone (uppermost Ordovician or lowermost Silurian). Also, as explained above, part of the undescribed species of "*Billingsites*" that are known to occur in the Upper Ordovician of southern Manitoba, northern Michigan, southwestern Ohio and adjacent parts of Indiana, and northeastern Iowa, and in the uppermost Ordovician or lowermost Silurian (Kallholn or Upper Leptaena, and Gastropod limestones) of the Dalarne area of central Sweden and the Ringerike area southwest of Oslo, Norway, doubtlessly represent this genus and part *Billingsites* s.s., but the published information in regard to them is not sufficient to allot them.

In summary then it can be stated that this genus is confined to the Upper Ordovician (Richmond and Gamaehian) in North America but is known to occur in southeastern Norway and in the

¹⁷ Billings (1862, p. 165) lists this species as occurring also on the south side of the St. Lawrence opposite Three Rivers (Trois Rivières), Quebec, and at Point Rich, Ontario, in Lake Huron, but it is doubtful if the forms occurring at these two localities are conspecific with the types, which came from Anticosti Island, as the three localities are widely separated. The single poorly preserved specimen from the Niagara of Delphi, Indiana, that Newell referred to this species is undoubtedly not congeneric with it.

Kallholn or Upper Leptaena limestone of Sweden where it is either uppermost Ordovician or lowermost Silurian in age. At present it is definitely known to occur only in southeastern Canada and southern Scandinavia, but in all probabilities it will eventually prove to be as widespread as *Billingsites* s.s., with which it is found in association. It seems probable that both of these genera developed out of *Probillingsites* after the close of the Middle Ordovician in an arctic or subarctic arm of the Atlantic and spread from there southward into northeastern North America and northwestern Europe during the latter part of the Upper Ordovician.

Genus LINDSTROEMOCERAS Miller, n. gen.

Plate V, Figs. 1-6

In his excellent study of the Ascoceratidae and the Lituitidae of the Silurian of Gotland, Lindström described two species of ascoceratoids from the zone of *Stricklandinia lirata* (lower Middle Silurian), a lower horizon than that which has yielded most of the Silurian ascoceratoids. He (p. 17) recognized that these forms presented certain striking differences from typical *Ascoceras* of the upper Middle Silurian of Bohemia, but he was too cautious to propose a generic name for them. Since the time of the publication of his memoir, our knowledge of the Ordovician mixochoanitic cephalopods has been increased many fold, and it now seems that, as is to be expected from the horizon they occupy, these lower Middle Silurian forms are clearly intermediate between part of the Upper Ordovician forms (*Schuchertoceras*) and part of the upper Middle Silurian forms (*Parascoceras*, described below); nevertheless, they appear to be generically distinct from both, and the generic name *Lindstroemoceras* is here proposed for them and L. [*Ascoceras*] *dolium* (Lindström) from Lindström's formation "b" near Visby, Gotland, is designed as the genotype.

Only the adoral obese part of the conch of this species is known, and our knowledge of it is based on two specimens. The conch is small, breviconic, and cyrtoceraconic, and the known portion is subovate in shape as it is short, obese, abruptly contracted orad, and more gradually so apicad; it is distinctly compressed laterally and is broadly elliptical in outline, but its ventral side is somewhat more convex than its dorsal. The adoral part of the conch is projected into a short neck-like extension, but its length and the nature

of the aperture are not known as neither of the types is complete adorally.

The surface of the internal mold is crossed by numerous small transverse ridges which curve slightly apicad as they cross the venter; they are somewhat less than 1 mm. apart. Both of the types retain traces of five septa; the adapical two, the septum of truncation and the basal septum are normal, saucer-shaped nautiloid septa, moderately convex apicad, and slightly inclined to the long axis of the conch; they slope orad from the venter. The next septum is close and almost parallel to the preceding ones in the ventral half of the conch, but near the mid-height of the conch it bends abruptly orad and continues in that direction to the center of the specimens where it bends abruptly dorsad and meets the dorsum near its mid-length. The next septum is very close and approximately parallel to the preceding one in the adapical half of the specimens, but near the center of them, where the preceding septum curves dorsad, this septum curves ventrad and orad and then gradually ceases to swing ventrad and curves dorsad; it meets the dorsum near the base of the adoral neck-like extension of the living chamber, far orad of the preceding septum. The adoral septum is not complete; it coalesces with the preceding septum just dorsad of the siphuncle and apparently becomes distinct from it again only in the extreme adoral part of the conch.

The nature of the siphuncle of the earlier stages of the phragmacone is not known, but in the adoral ovoid expansion of the conch it is ventral in position and is moderately small but it gradually increases in diameter orad. The septal necks apparently are short and strongly recurved. The segment of the siphuncle between the septum of truncation and the basal septum is expanded within the camera, and the connecting ring is subfusiform in shape; those of the adoral segments are not preserved in either of the types, but they probably were subnummuloidal in shape.

The general shape of the conch and the sutures of *Ascoceras rochleatum* Lindström of the soft gray shale (Lindström's formation "b" = lower Middle Silurian) near Visby, Gotland, are strikingly similar to that of the above-described genotype, and therefore that species is regarded by the writer as belonging to the genus under consideration although its conch is strongly annulated. The single fragmentary specimen found in the "red limestone [upper Middle Silurian] at Holms haller in Wamlingbo," Gotland,

and regarded by Lindström as a doubtful variety of this species only because of a similarity in surface sculpture, probably does not belong to this genus but to *Aphragmites*, and no other species is known to the writer that should be referred to this genus.

The fact that the adoral expansion of the conch of this genus is very short and obese and is subovoid in shape is indicative of a close relationship to the Upper Ordovician and Lower Silurian mixochoanites, but the lateral compression, adapical attenuation, and moderately long and distinct adoral extension of the living chamber indicate a relationship to the upper Middle Silurian ascoceratoids; the genus seems to be distinctly intermediate between *Schuchertoceras* of the Upper Ordovician and probably the Lower Silurian and *Parascoceras* of the upper Middle Silurian. The presence of a basal septum serves to distinguish it from *Billingsites* of the Upper Ordovician (and possibly the Lower Silurian) and *Ascoceras* s.s. and *Aphragmites* of the upper Middle Silurian.

Genus PARASCOCERAS Miller, n. gen.

Plate VII, Figs. 3-12

Of the numerous ascoceratoids known from the upper Middle Silurian, only one¹⁸ species, *Ascoceras fistula* Lindström of the uppermost formation (Lindström's "stratum h") of Gotland, possesses a so-called basal septum, i.e., a septum between the septum of truncation and the first sigmoidal septum. Lindström called attention to this fact and he realized that the possession of this septum indicated a close relationship between this species and the forms from the lower Middle Silurian termed *Lindstroemoceras* above, but he apparently attached little importance to it. The significance of this basal septum is treated of elsewhere in this report but perhaps it should be mentioned here that the presence or absence of it enables us to distinguish two closely related stocks

¹⁸ The specimen, showing two septa apicad of the first sigmoidal one, that Barrande (1877, pp. 98-99, pl. 491, figs. 3-7) described and figured and referred to *Ascoceras murchisoni* was regarded by Lindström (pp. 18-19) as indicating a close relationship between that species and *Ascoceras fistula*; but in the writer's opinion that specimen is either abnormal, in that truncation accidentally took place slightly apicad of the adoral end of the orthochoanitic part of the conch instead of at the junction with the cyrtochoanitic part, or it is an immature individual in which the adapical portion of the conch had not been broken off as yet and only the two adoral camerae of it were preserved. The septum regarded by Lindström as homologous with the so-called basal septum of *A. fistula* is not close to the first sigmoidal septum but is relatively far from it, and the segment of the siphuncle between the two was undoubtedly cylindrical and not nummuloidal.

that differentiated in the Ordovician and evolved along parallel lines until near the close of the Middle Silurian, when both became extinct. It should also be repeated here for the sake of emphasis that as far as is now known, the septum of truncation in the mixochoanitic cephalopods (with the possible exception of *Chonanoceras*) marks the junction of the orthochoanitic part of the conch with the cyrtochoanitic, and therefore the presence of a basal septum can not be explained merely by assuming truncation along a more posterior septum; its development was far more complicated than that.

As is obvious from what has been stated above, this species represents a genus that is quite distinct from typical *Ascoceras*, though it resembles that form in many respects, and the name *Parascoceras* is here proposed for it; *P. [Ascoceras] fistula* (Lindström), the only known species, is the genotype. That form is known to occur only in one horizon in Gotland, but it is comparatively abundant there and Lindström figured a slab only two or three inches square that contains twenty-one more or less perfect representatives of it.

As is probably the case with most of the other mixochoanitic cephalopods, the conch of this species consists of two distinct parts. The adapical tubular part, termed the "Nautiloid stage of growth" by Lindström because its septa are normal saucer-shaped disks approximately transverse to the long axis of the conch, is here called the orthochoanitic part. The adoral portion of the conch in which all of the septa but the so-called basal septum are strongly sigmoidal, is termed the "Ascoceras stage" by Lindström, but it is here called the cyrtochoanitic part of the conch; it includes the living chamber as well as the cyrtochoanitic part of the phragmacone of mature specimens. The septum of truncation apparently formed the junction of these two parts, and the two have never been found connected; nevertheless, the similarity of their size and surface sculpture, the position of their siphuncles, and the fact that the two are found only in very close association indicate that they represent the same species, and that the adapical portion of the conch was truncated during the life of the individual.

The orthochoanitic part of the conch is long, narrow, tubular, and almost straight, and it is only very gradually expanded orad; it is circular or nearly so in cross section. The protoconch is not known, and the adapical end of the conch is bluntly rounded. The

surface of the conch is crossed by numerous, low, rounded, inconspicuous transverse ridges, which are considerably less than 1 mm. apart and which curve slightly apicad as they cross the venter; the surface of these ridges and the concave spaces between them is finely transversely striate. The septa are moderately convex apicad and are approximately transverse to the long axis of the conch but slope slightly orad from the venter; the sutures are simple and straight and approximately circular. They are moderately close together, but the distance between them increases progressively orad. The siphuncle is ventral in position and is small. The septal necks are very short, but they are not recurved and the connecting rings are not expanded transversely within the camerae but are cylindrical in shape.

The adoral or cyrtochoanitic part of the conch at maturity consists of the living chamber and four camerae. It is slightly curved longitudinally and is long, narrow, and subcylindrical in shape, but it is somewhat compressed laterally and is therefore broadly elliptical in cross section. Its maximum transverse dimensions are attained somewhat apicad of its mid-length, and it is contracted slightly both orad and apicad of there. The adoral end of the living chamber is projected orad into a long cylindrical neck-like extension, which is circular in cross section and constitutes about two-sevenths of the total length of the living chamber. The surface of the conch is marked by numerous small transverse ribs about $\frac{1}{3}$ mm. apart; these curve slightly apicad as they cross the venter, and they are finely striate. The septum of truncation and the basal septum are very similar to the septa of the orthochoanitic part of the conch and are normal, saucer-shaped, nautiloid septa that are approximately transverse to the long axis of the conch but slope slightly orad from the venter. The next septum is approximately parallel to the basal septum in the ventral half of the conch, but in the dorsal half it curves strongly orad and then slightly ventrad, and, near the mid-length of the specimen, curves strongly dorsad to meet the dorsum. With the exception of a single specimen figured by Lindström, in which the first two sigmoidal septa are entire, the two adoral septa are not complete centrally as they unite and then coalesce with the preceding septum just dorsad of the siphuncle and separate from it only in the adoral half of the conch; they extend the phragmacone along the dorsum to the base of the neck-like adoral extension of the living chamber

mentioned above. This coalescing of the sigmoidal septa is visible only in sectioned specimens, for the edges of all these septa are distinct and their sutures do not coalesce. It is interesting to note in this connection that in senile representatives of this genus, as in those of *Ascoceras* s.s. and *Pseudascoceras*, an additional septum, here termed an *adventitious septum*, is added in the posterior end of the living chamber close to the adoral sigmoidal septum; no trace of it is visible along the Dorsum as it coalesces with the preceding septum in the dorsal part of the conch. The siphuncle of this cyrtochoanitic part of the conch is ventral in position and is moderately small, but its segments are expanded transversely within the camerae. The septal funnels apparently are short and strongly recurved, and the connecting rings are subspherical in the posterior part of the specimen but become much shorter in the adoral part, where they are asymmetrically subnummuloidal. The septal necks and connecting rings of the adventitious septum present in senile individuals are similar to those of the preceding septa.

As mentioned above, no species is known to the writer that is congeneric with this genotype, and its closest relatives seem to be the three forms discussed below and referred to a new genus, *Pseudascoceras*, in which the basal septum apparently was resorbed before the individuals attained maturity. It is believed by the writer that both this form and *Pseudascoceras* evolved from *Lindstroemoceras* of the lower Middle Silurian, which is a shorter and more obese form with a much shorter and less distinct neck or adoral extension of the living chamber. The presence of a basal septum serves to distinguish the genus under consideration from other similar genera.

Genus PSEUDASCOCERAS Miller, n. gen.

Plate V, Figs. 7-21

As mentioned above in the discussion of *Parascoceras*, three of the numerous species of ascoceratoids described by Lindström from the upper Middle Silurian of Gotland apparently possessed a basal septum during part of their development but resorbed it before attaining maturity. These forms then are closely related to *Parascoceras* and *Lindstroemoceras*, which retained the basal septum throughout life, but externally they appear to resemble much more closely *Ascoceras* s.s., which never possessed a basal

septum. They obviously are generically distinct from all three of the genera mentioned, and the generic name *Pseudascoceras* is here proposed for them and *P. [Ascoceras] decipiens* (Lindström) of the uppermost formation of Gotland (Lindström's "stratum h") is designated as the genotype.

That species is known from numerous specimens from various localities on the island of Gotland. Its conch consists of two distinct parts; the adapical one is orthochoanitic, the adoral cyrtochoanitic. The former was generally broken off during the life of the individual, but both parts are known and have been found connected in immature representatives.

The orthochoanitic part of the conch is moderately long, narrow, and very gradually expanded orad; it is distinctly curved exogastrically, but the amount of curvature decreases adorally. The protoconch is not known, and the bluntly rounded apex of the conch does not show any distinct cicatrix. The surface of this orthochoanitic part of the conch is finely transversely striate and in addition bears small, low, rounded, indistinct longitudinal ridges. The septa are saucer-shaped and moderately convex apicad. They are rather close together, but the distance between them varies somewhat and in general increases progressively orad. They are transverse to the long axis of the conch, and the sutures are therefore simple circles. The siphuncle is small, circular in cross section, and ventral in position. The septal necks are short but are not recurved, and the connecting rings are cylindrical in shape; therefore the segments of the siphuncle are not expanded appreciably within the camerae.

The adoral or cyrtochoanitic part of the conch of mature specimens consists of the living chamber and four camerae. It is slightly curved exogastrically, and is long, narrow, and subcylindrical in shape, but it is slightly compressed laterally and is therefore broadly elliptical in cross section. It is nearly straight along the dorsum but is convex along the venter. Its maximum transverse dimensions are attained near the mid-length of the living chamber proper, and it is somewhat contracted apicad and slightly so orad of that point. The adoral end of the living chamber is projected into a long narrow tubular neck that is circular in cross section and is distinctly inclined to the long axis of the conch; its maximum length and the nature of the aperture are not known, but it is at least two-fifths as long as the living chamber proper. The

entire cyrtochoanitic part of the conch is finely transversely striate and is marked also by small, low, rounded longitudinal ridges. The ornamentation varies slightly in the different parts of the conch; it is finer on the ventral and apical portions of the specimens and is coarser on the neck. The septum of truncation is asymmetrically subconical and is inclined to the long axis of the conch; it slopes orad from the venter. The next septum is approximately parallel to it in the ventral three-fourths of the conch, but its dorsal part curves abruptly orad and then somewhat ventrad and continues in that direction to the center of the living chamber proper, whence it curves abruptly dorsad to meet the dorsum. The next four septa are not complete centrally as they unite and then coalesce with the first sigmoidal septum just dorsad of the siphuncle and become distinct from it again only in the adoral half of the conch; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. This coalescing of the septa is visible only in sectioned specimens, for the edges of all the sigmoidal septa and therefore the sutures are distinct. Lindström observed a thin deposit that he believed to be organic in origin on the inside of the living chamber extending a short distance each side of the junction of the adoral septum with the dorsum, but the significance of this is not understood. The siphuncle of this part of the conch is small at its passage through a septum, but the segments are greatly expanded transversely within the camerae. A small oblique narrow tube connects the siphuncles of the two parts of the conch. The septal necks are short and strongly recurved. The connecting ring between the septum of truncation and the first sigmoidal septum is almost square in longitudinal section, but near its mid-length it bears a constriction, comparable to that observed in *Schuchertoceras*, but angular on the ventral side and rounded on the dorsal. This segment of the siphuncle is more than twice as long as the succeeding ones, and the constriction near its mid-length is interpreted by the writer as a vestige of a septum—comparable to the basal septum of *Parascoceras* and *Lindstroemoceras*—that was present during part of the development of the individual but was resorbed before maturity. This constriction is therefore regarded as one of the most significant of the generic characters, and it indicates that this form is much more closely related to the two genera mentioned above than to *Ascoceras*, to which it is strikingly similar external-

ly. The adoral four segments of the siphuncle are much shorter and are subnummuloidal in shape; they become progressively shorter orad.

It is exceedingly important to note that a senile individual of this species has been described by Lindström in which as many as four adventitious septa are present "in the adapical part of the living chamber." These are all normal, saucer-shaped nautiloid septa, strongly convex apicad, and slightly inclined to the long axis of the conch; they slope orad from the venter. The septal necks of the first two of these septa are strongly recurved, and the connecting ring of the first is asymmetrically subnummuloidal in shape, whereas that of the next is asymmetrically fusiform. The septal necks of the two adoral septa, however, are not recurved, and their connecting rings are only slightly expanded transversely within the camerac. The important thing to note in this connection is that this particular individual has reverted to an orthochoanitic form after passing through a cyrtochoanitic stage. The significance of this is more or less of an open question, but it seems to the writer that this demonstrates that the distinction between cyrtochoanitic and orthochoanitic forms is not as great as most paleontologists are inclined to believe.

It should also be noted that other representatives of this species have been described by Lindström that indicate that the adoral part of the conch was completed by the individual before the sigmoidal septa were developed and truncation occurred. One specimen represents an immature individual which had secreted only the first of the sigmoidal septa and had not broken off the adapical portion of the conch; the adoral connecting ring of this specimen bears the characteristic constriction near its mid-length and demonstrates that, as would be expected, the assumed basal septum was resorbed before the sigmoidal septa were formed.

As is indicated by the name and has been explained above, representatives of this genus can be differentiated from typical *Ascoceras* only by means of internal structures, i.e., vestiges of a basal septum; therefore only those species in which the details of the siphuncle are known can be definitely allotted. As far as the writer has been able to ascertain, only *Ascoceras siphon* Lindström and *Ascoceras gradatum* Lindström, both of the Upper Middle Silurian (Lindström's "stratum h") of Gotland have been shown to possess similar vestiges of a basal septum and therefore to be-

long to this genus. In the future it may be possible to show that some of the numerous species at present assigned to *Ascoceras*, actually represent this genus, but until representatives of those forms have been sectioned and studied, it will be best to leave them in the genus to which they have been referred.

(Genus ASCOCERAS Barrande 1847

[= *Cryptoceras* Barrande (1846) 1847, but not *Cryptoceras*
D'Orbigny 1850]

Plate VI, Figs. 1-6; Plate VII, Figs. 1,2; Plate VIII, Figs. 10,11

A detailed summary of the development of our knowledge of this genus has been ably presented by Barrande and later by Lindström, and therefore it will suffice here to mention only the more significant points. In 1846 Barrande announced the discovery of this genus and proposed the name *Cryptoceras* for it; however as he then stated only that it is a "genre que nous avons créé pour classer des formes auparavant inconnues et très-bisarrés," he failed to establish the name, for this statement can not be considered a generic diagnosis and it is not accompanied by an illustration. In the following year Barrande abandoned the name *Cryptoceras* as he believed it was too similar to *Cryptocerus* Latreille, a hymenopterous insect, and he proposed to call his genus *Ascoceras*; this time he gave a concise diagnosis of the genus and established its name as *Ascoceras*. It was not necessary for him to abandon *Cryptoceras*, but in as much as he did so before it was established, i.e., while it was a *nomen nudum*, that term can not be revived on the grounds of priority, as has recently been suggested by Schindewolf (1929, p. 171). Furthermore, since in the same publication in which *Ascoceras* is established, it is stated that Barrande's term *Cryptoceras* referred to the same genus, that name also is established, and it must be regarded as a direct synonym of *Ascoceras*; it was "stillborn and can not be brought to life." According to Barrande (1867, p. 335) the above-mentioned original diagnosis of *Ascoceras* was "imprimée d'abord dans *Oesterr. Blätt. für Litt. u. Kunst* en 1847 et ensuite dans *Haidinger's Berichte III*, p. 268," 1848. The writer has not been able to locate a copy of the first of these two references, but Barrande's statement is confirmed by the editor of the second.

In manuscript prepared in 1847 but not published until 1850,

D'Orbigny¹⁹ unaware of Barrande's earlier use of the term *Cryptoceras*, employed it for an entirely different group of nautiloids, according to him known to be represented by one Devonian and one Carboniferous species; and in the second edition of Woodward's *A manual of the Mollusca* . . ., London, 1866 (p. 189). *Ascoceras* Barrande is inadvertently listed as a synonym of *Cryptoceras* D'Orbigny. In his *Prodrome de Paléontologie* . . . (vol. 1, p. 58 and p. 114, 1850), D'Orbigny listed as the two species on which he had based his genus *Nautilus subtuberculatus* G. and F. Sandberger of the Devonian of Germany and *Nautilus dorsalis* Phillips of the Carboniferous of England. In 1883 Hyatt (p. 283) designated the former as the type of the genus, which, however, he regarded as a synonym of *Temnocheilus* M'Coy 1844; *Nautilus* (*Temnocheilus*) *coronatus* M'Coy of the Carboniferous of Ireland is the type of *Temnocheilus*. The types of these two genera are not very similar, and the modern refinement in limiting nautiloid genera makes it expedient to resurrect D'Orbigny's genus, but in view of the fact that the name employed by D'Orbigny was pre-occupied, it is necessary to coin a new generic name for the genus, and it is here proposed to call it *Nassauoceras*; the type species, *N.* [*Nautilus*] *subtuberculatus* G. and F. Sandberger²⁰, came from the Devonian of Nassau, a former duchy of Germany.

In 1855 Barrande for the first time named and described a species of *Ascoceras*, *A. bohemicum* of the upper Middle Silurian of Bohemia (since found also in the upper Middle Silurian of Gotland), and it is the type of his genus. Only the adoral or cyrtchoanitic part of the conch of this species is known; it has been described in detail by Barrande, Lindström, and Foord, and therefore the following concise description will suffice here.

The known portion of the conch of this species, the adoral cyrtchoanitic part, in typical, mature specimens consists of the living chamber and the adoral four (sometimes five) camerae of the phragmacone. It is subcylindrical in shape but is convex exteriorly and, as it is compressed laterally, is oval in cross section; it is more narrowly rounded ventrally than dorsally. The adoral fifth

¹⁹ D'Orbigny, Aleide, Cours élémentaire de Paléontologie et de Géologie stratigraphiques, vol. 1, p. 286, Paris, 1849 (not published until 1850 according to Barrande [1867, p. 335]).

²⁰ Originally described by Sandberger, Guido, and Sandberger, Fridolin, Die Versteinerungen des rheinischen Schichtensystems in Nassau, pp. 133 134, pl. 12, figs. 3a-3e, Wiesbaden, 1850-1856.

of the living chamber is projected aperturally into a neck-like extension that is circular in cross section and is inclined to the long axis of the conch; the aperture is circular and is directly transverse to the long axis of the neck and therefore inclined to that of the conch. The test is moderately thick and is finely transversely striate. The septum of truncation is a normal saucer-shaped nautiloid septum that is only slightly convex apicad and is distinctly asymmetrical; it slopes orad from the venter and is therefore inclined to the long axis of the conch. The next septum is not far orad of the septum of truncation and is approximately parallel to it in the ventral four-fifths of the conch, but slightly below the dorsum it curves orad and ventrad and continues in that direction to near the mid-length of the living chamber proper, where it curves abruptly dorsad to meet the dorsum. The next four septa are not complete centrally as they unite and then coalesce with the first sigmoidal septum just dorsad of the siphuncle and become distinct from it again only in the adoral half of the specimens; they extend the phragmacone along the dorsum almost to the base of the adoral neck of the living chamber. The maximum dorso-ventral thickness of the adoral portion of the phragmacone is attained somewhat orad of the mid-length of the living chamber proper along the third camera, and the adoral segment of the phragmacone is much smaller than the preceding ones. The details of the coalescing of the septa vary in different individuals and apparently in some cases (see Lindström, pl. 3, and Barrande, pl. 494) it can be observed only in sectioned specimens as the edges of the septa and therefore the sutures are distinct. However, Barrande figured one specimen (pl. 93) in which the two adoral sutures coalesce laterally, and another (pl. 513) in which all of the sigmoidal septa coalesce successively along the lateral sides of the conch. The sutures of the sigmoidal septa curve slightly apicad on the dorso-lateral sides of the conch and form broad, shallow median lobes along the dorsum; these however become less prominent adorally. The siphuncle of this part of the conch is ventral in position and is moderately large, but it apparently decreases in diameter adorally. The septal necks are fairly short and are strongly recurved; the connecting rings are greatly expanded transversely within the camerae, and the segments of the siphuncle are asymmetrically subnummuloidal in shape.

As mentioned above, the earlier stages of the phragmacone of

this species are not known, but they doubtlessly were very similar to those of *Ascoceras manubrium* Lindström and *Ascoceras lagena* Lindström, which have been found in connection with the adoral portion of the conch. The adapical or orthochoanitic part of the conch of both of those species is long, narrow, very gradually expanded orad, and gently curved exogastrically. Neither the protoconch nor the adapical end of the phragmacone is known. The sutures are simple circles and the septa are normal saucer-shaped nautiloid septa moderately convex apicad and approximately transverse to the long axis of the conch; they are fairly close together in the adapical part of the conch, but the distance between them increases progressively orad and equals or exceeds the diameter of this portion of the conch near its junction with the cyrtchoanitic portion. The siphuncle is small and is located close to the ventral wall of the conch. The septal necks are short but are not recurved, and the connecting rings are not expanded appreciably within the camerae but are cylindrical in shape.

The conch of the above described genotype, *Ascoceras bohemicum*, is somewhat larger than that of most of the forms that have been referred to this genus, but as near as the writer has been able to determine from the literature and the material available for study, the following species possess the same general characters and should therefore be referred to *Ascoceras* s.s.: *A. bronni* Barrande²¹, *A. munchisoni* Barrande, *A. singulare* Barrande, and *A. verneuili* Barrande, all of Barrande's division "e2" of stage E (= Eß of Kettner and Kodym) of the upper Middle Silurian of Bohemia; *Ascoceras* cf. *A. munchisoni* (identified by Perner, 1922, p. 60) of E1γ, that is, the passage beds (= Dubius beds of Perner) between e1 and e2 of Bohemia; *A. pupa* Lindström, *A. reticulatum* Lindström, *A. ampulla* Lindström, *A. collare* Lindström, *A. lagaena* Lindström, *A. manubrium* Lindström, and *A. cucumis* Lindström, all of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland; *A. barrandii* Salter of the Upper Ludlow of England; *A. southwelli* Worthen of the Port Byron of Illinois; *A. croneisi* Foerste of the Racine of Wisconsin; *A. indianensis* Newell of the Huntington of northern Indiana; and *A. townsendi* Whiteaves of the Guelph of southeastern Ontario. Also, the affinities of the following forms, which are

²¹ The forms originally described by Barrande as *Ascoceras* (*Aphragmites*) *salteri* were later correctly included by him in *Ascoceras bronni*.

based upon poorly preserved material and are therefore incompletely known seem to be with this genus rather than any of the other genera discussed in this report: *A. vermiforme* Blake from the Lower Ludlow (and Upper Ludlow?) of England; the specimen from the Upper Ludlow of Whitecliffe, England, that Blake (p. 208) incorrectly identified as *A. bohemicum*; the specimen from the Huntingdon of Delphi, Indiana, that Newell (p. 484) incorrectly identified as "*Ascoceras Newberryi* Billings"; and the various forms from the upper Middle Silurian of Gotland figured by Lindström (pl. 4) as *Ascoceras* spp. Additional material may enable us to allot these forms definitely in the future, but for the present it seems best to leave them in the genus to which they have been referred. In summary it can be stated that *Ascoceras* s.s. is known to be represented in the upper Middle Silurian of Bohemia, Gotland, England, Ontario, Indiana, Illinois, and Wisconsin. *A. townsendi* Whiteaves (figured on plate VIII, figures 10, 11, of this report) is the last representative of the group known to occur in North America.

The genus *Ascoceras* can be readily distinguished from *Glossoceras* by its simple aperture; from *Aphragmites* by its non-anululated conch; from *Billingsites* by its laterally compressed, sub-cylindrical conch with circular aperture and longer, more distinct neck; and from *Schuchertoceras*, *Lindstroemoceras*, *Parascoceras*, and *Pseudascoceras* by the absence of a basal septum or vestiges of it.

Genus APHRAGMITES Barrande 1865

Plate VIII, Figs. 1-9

As is indicated by its name, this genus was created by Barrande as a result of a misconception, i.e., during much of his study of the ascoceratoids, he believed that one group of them was essentially without septa. As early as 1855 he mentioned this view and figured *Ascoceras buchi* Barrande of the upper Middle Silurian of Bohemia as typical of the group, which, however, he did not name until 1865, when in a volume of plates (explanation of pl. 94) he wrote as follows: "Nous établissons le sous-genre *Aphragmites* pour comprendre les deux espèces: *Buchi* et *Salteri*, dans lesquelles il ne paraît exister qu'une seule cloison permanente, terminant la grande chambre, sans cloisons intermédiaires." In the text to accompany these plates, published two years later, he (pp. 366-372)

raised *Aphragmites* to generic rank, discussed it at some length, and described the two species that he had referred to it. However, in 1877, when he completed his voluminous masterpiece on the cephalopods, he (p. 94) renounced this genus, stating "nous concevons, que l'animal résorbait toutes les cloisons adossées à la grande chambre, à chacune des époques périodiques, qui correspondent à sa croissance et à l'agrandissement de son habitation. . . . En adoptant cette conception . . . nous avons été amené à regarder les coquilles dénuées de toute cloison interne et par ce motif, nommées par nous *Aphragmites*, comme représentant l'état transitoire, qui correspond à la transformation en question. Nous sommes donc obligé de considérer le genre *Aphragmites* comme désormais sans raison d'être et nous devons déterminer quelles sont les espèces du genre *Ascoceras*, auxquelles les 2 formes nommées: *Aphragm. Buchi* et *Aphragm. Salteri*, doivent être rapportées. Nous allons exposer pour chacune de ces 2 formes les motifs qui nous induisent à les incorporer, la première dans l'espèce *Ascoc. Deshayesi* et la seconde dans l'espèce *Ascoc. Bronni*."

In 1883, Hyatt (p. 279) resurrected this genus, stating that he preferred Barrande's earlier opinion in regard to it, and in 1900 (p. 516) he recapitulated this view. Zittel (1885, p. 371) likewise took cognizance of it and considered it a valid genus, though he was cautious enough to mention Barrande's ultimate conclusions in regard to it.

However, it remained for Lindström to demonstrate the true nature of this misunderstood "genus" and to show that it in reality represented a developmental stage of *Ascoceras*, i.e., as an individual of that genus approached maturity it apparently underwent a metamorphosis and suddenly increased the diameter of the conch that it was secreting; the walls of this expanded adoral portion of the conch were then completed aperturally while septa were being formed in the narrow adapical portion of the conch. At or shortly after this stage in the development, the adapical septate portion of the conch was cast off and septa were formed in the apical and dorsal parts of the remaining (the expanded) portion of the conch. Just before these later septa were secreted, the conch was in the "Aphragmites stage" of development.

In spite of the fact that "*Aphragmites*" as originally conceived represented only a developmental stage of *Ascoceras*, it now seems desirable to retain the generic name; for as has already been noted

by Foerste (1924, pp. 216-217), the conch (and the internal mold) of *Ascoceras buchi*, which has always been regarded as the type of *Aphragmites* and is here selected as such, is prominently annulated transversely, whereas that of typical *Ascoceras* is smooth or finely striate.

Only the adoral, expanded, or cyrtocchoanitic part of the conch of the genotype, *Aphragmites* [*Ascoceras*] *buchi* (Barrande)²² of stage E of the upper Middle Silurian of Bohemia, is known, and as it has been described in detail by Barrande (1867, pp. 361-362 and 370-371; 1877, pp. 94-95), the following concise description will suffice here. The earlier stages of the phragmacone, the orthocchoanitic part of the conch, in all probability, were comparable to those of *Ascoceras* s.s.

The known portion of the cyrtoceraconic conch of this rare species consists in mature specimens of the living chamber and the adoral four camerac of the phragmacone. It is moderately small and is subfusiform in shape, but it is compressed laterally and is therefore elliptical in cross section. It is almost straight (very slightly convex) along the dorsum but is strongly gibbous along the venter; its maximum transverse dimensions are attained near its mid-length and it is rather strongly contracted both apicad and orad of that point. Its adoral portion is projected aperturally into a neck-like extension that is about one-third as long as the living chamber proper, is distinctly inclined to the long axis of the conch, and is circular in cross section. The aperture is simple and, as it is transverse to the long axis of the neck, is circular in outline. The test is moderately thin, and both it and the internal mold are strongly annulated transversely. The narrowly rounded annulae are about the same size as the intermediate grooves and are directly transverse to the long axis of the conch. They are about $\frac{1}{2}$ mm. high and $1\frac{1}{2}$ mm. apart in the central portion of the specimens, but they become less prominent and more closely spaced both adapically and adorally; they are rather faint and only about $\frac{1}{2}$ mm. apart on the adoral neck. The septum of truncation is a normal, saucer-shaped nautiloid septum that is slightly inclined to the long axis of the conch; it slopes orad from the venter. The dorsal part of the next septum is bent strongly orad and slightly ventrad so as to form a very prominent deep dorsal saddle before it meets the dorsum slight-

²² This species and *Ascoceras deshayesi* Barrande are identical, and the older name is retained.

ly apicad of the mid-length of the living chamber proper. The nature of the rest of the septa in the ventral half of the conch is not known, but they probably unite and then coalesce with the preceding septum slightly dorsad of the siphuncle. Anyhow, they are not complete centrally, and they separate from the preceding septum and then from each other in the adoral half of the specimens; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. The maximum dorso-ventral thickness of this adoral dorsal portion of the phragmacone is attained somewhat orad of the mid-length of the living chamber proper along the adapical end of the adoral camera or the adoral end of the preceding one. The sutures of the second and third of these sigmoidal septa curve slightly apicad on the dorso-lateral sides of the conch and form shallow median lobes along the dorsum. All of these sigmoidal sutures appear to coalesce laterally near the same point in the adapical third of the specimens; unfortunately their nature on the ventral side of the conch is not known. The siphuncle is ventral in position and is moderately small at its passage through a septum, but it appears to be expanded within the camerae; nothing further is known in regard to it. The siphuncle and the ventral traces of the sigmoidal septa of this genus are probably not greatly different from those of *Ascoceras* s.s.

As near as can be told from the literature, the following species possess the same general characters at this genotype and should therefore be grouped together with it under the generic name *Aphragmites*: *Ascoceras goldfussi* Barrande, *A. invertens* Barrande, *A. keyserlingi* Barrande, *A. amoenum* (Barrande)²³, and *A. konincki* Barrande, all of the same general horizon and locality as the genotype, i.e., Barrande's division "e2" of stage E (= E β of Kettner and Kodym) of the upper Middle Silurian of Bohemia.

It seems likely that this genus arose from *Ascoceras* or its immediate progenitor by the increased prominence of certain of the transverse striae, and it is perhaps significant that it is not known to occur outside of Bohemia, with the possible exception of the single fragmentary specimen from the upper Middle Silurian of Gotland mentioned above in the discussion of *Lindstroemoceras*. It should also be noted in this connection that at least one of the known representatives of *Billingsites* [*B. costulatus* (Whiteaves)]

²³ This form was described by Barrande as a variety of *Ascoceras keyserlingi*, but it is here regarded as a distinct species.

bears rather prominent transverse ridges on the exterior of its conch, but the internal mold is smooth; also transverse annulations were developed in at least one other group of the Mixochoanites, *Lindstrocmoceras* of the lower Middle Silurian of Gotland.

The conch of this genus is strikingly similar to that of *Ascoceras*, from which it differs chiefly in being annulated, and it can be differentiated from other similar genera by the criteria mentioned at the close of the discussion of that genus.

Genus GLOSSOCERAS Barrande 1865

Plate VIII, Figs. 12-25

This genus was established by Barrande in a volume of plates (explanation of plate 94) as a subgenus of *Ascoceras*, and defined as follows: "Nous établissons le sous-genre *Glossoceras*, pour comprendre les formes dont l'ouverture est contractée par une languette, comme celle des *Lituil. Ophioceras*, et reproduit à peu près le type de l'ouverture des *Phragmoceras* et *Gomphoceras*." The text to accompany these plates did not appear until two years later, and in it Barrande (pp. 372-375) raised *Glossoceras* to generic rank, discussed it at some length, and described in detail one species and a variety of it (here regarded as two distinct species). Since then Barrande, Hyatt, Zittel, Foord, and other authors have discussed this genus at various times, but only Lindström has added appreciably to our knowledge of it. He found a representative of it in the upper Middle Silurian of Gotland and studied its internal structure in detail, which Barrande had failed to do.

The single species recognized by Barrande, *Glossoceras gracile* (Barrande) of division "c2" of stage E (= E β of Kettner and Kodym) of the upper Middle Silurian of Bohemia, is the type of the genus. Only the adoral or cyrtochoanitic part of its conch is known, but the earlier stages of its phragmacone, i.e., the orthochoanitic part of the conch, in all probability, were comparable to those of *Ascoceras* s.s. In as much as this genotype has been described in detail by Barrande the following concise description will suffice here.

The known portion of the conch of this species, the adoral or cyrtochoanitic part, consists in mature specimens of the living chamber and the adoral six camerae of the phragmacone. It is long and slender and is somewhat curved exogastrically; it is compressed laterally and, being more narrowly rounded ventrally than

dorsally, is oval in cross section. The adoral fifth of the living chamber is projected aperturally into a long, narrow cylindrical neck that is circular in cross section; this neck is distinctly curved endogastrically, and therefore the specimens as a whole are sigmoidal in shape. The dorsal side of the aperture is projected as a moderately long and narrow subtriangular lobe, which is curved rather strongly ventrad; the lateral and ventral sides of the aperture are approximately transverse to the long axis of the neck and are nearly straight, but there appears to be a tendency for them to become slightly concave and for small ventro-lateral lobes to be developed—such lobes are very distinct in the other two known species of this genus. The test is ornamented by faint longitudinal and transverse lines, which give it a reticulate appearance. The septum of truncation is a normal nautiloid septum, but it is rather strongly convex apicad and, as it slopes orad from the venter, is distinctly inclined to the long axis of the conch. The rest of the septa are not well preserved in any of the typical mature specimens that have been figured, but apparently the dorsal part of the septum just orad of the septum of truncation curves strongly orad and somewhat ventrad so as to form a long deep dorsal saddle; this septum then curves abruptly dorsad and meets the dorsum only slightly apicad of the mid-length of the living chamber proper. The nature of the rest of the septa in the ventral half of the conch of this species is not known as Barrande failed to detect them, but they probably are not greatly different from those of *Glossoceras lindstroemi*, n. sp., discussed below. The five adoral sigmoidal septa are not complete centrally, and they separate from the preceding septum and then from each other in the adoral half of the specimens; they extend the phragmacone along the dorsum to the base of the adoral neck of the living chamber. All of the sutures of these septa appear to coalesce successively below the dorsum along the lateral sides of the conch; they probably are distinct along the ventral side of the conch, but Barrande's figures do not show them. Very little information is available in regard to the siphuncle of this species, but it is ventral in position and is small at its passage through the septum of truncation but appears to be expanded within the adjacent camera; it probably is not very different from that of *Glossoceras lindstroemi*, discussed below.

As mentioned above, Lindström (pp. 33-34, pl. 5, figs. 44-52)

discovered a representative of this genus in the upper Middle Silurian of Gotland and studied and described it in his masterly way. He referred his specimens to "*Glossoceras gracile* var. *curta* Barrande" but recognized that they presented certain differences from that form, e.g., in the shape of the tongue-like lobe on the dorsal side of the aperture, and it now seems desirable to regard them as representing a distinct species; it is here proposed to call it *Glossoceras lindstroemi*, in honor of its discoverer. The known portion of its conch, the adoral or cyrtochoanitic part, is shorter than that of the genotype and consists of only four or five camerae of the phragmacone and the living chamber, but otherwise the two species are not greatly different, and our knowledge of the internal structure of this form will serve in lieu of that of the genotype. The first sigmoidal septum is complete and is essentially like that of the genotype described above; the rest of the adoral sigmoidal septa unite immediately dorsad of the siphuncle and then coalesce with the preceding septum; they become distinct from that septum again only in the adoral half of the specimens. The siphuncle of this portion of the conch is small at its passage through the septa, but its segments are greatly expanded transversely within the camerae, and the septal necks apparently are strongly recurved. The segment of the siphuncle between the septum of truncation and the first sigmoidal septum is subglobular in shape, but the other adoral segments are much shorter and are asymmetrically subnummuloidal.

As near as the writer has been able to tell from the literature, only three species of this genus are known, and all three are strikingly similar and are confined to the upper Middle Silurian. They are: *Glossoceras gracile* (Barrande) (the genotype) and *G. curtum* (Barrande)²⁴ of division "e2" of stage E (= E β of Kettner and Kodym) of the upper Middle Silurian of Bohemia, and *G. lindstroemi* Miller (named above and described by Lindström, 1890, pp. 33-34, pl. 5, figs. 44-52) of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland.

The small specimen from the oölitic limestone of division "e1" of stage E of the Middle Silurian of Bohemia, that Barrande (1877, p. 241) referred to *Glossoceras gracile*, only because of its slender

²⁴ This form was described by Barrande as a variety of *Glossoceras gracile*, but it is here regarded as a distinct species.

form and the reticulate ornamentation of its conch, is so incomplete and so inadequately described that it is not now possible to place it generically; the adoral part of the specimen is not preserved, and the only septum that is discernible from Barrande's figures is the septum of truncation. Narrow conchs and reticulate surface ornamentation are now known to occur in several genera of the mixochoanitic cephalopods.

The specimen from the upper Middle Silurian (Chicotte) of Anticosti Island that Billings (1866, p. 60) described as *Glossoceras desideratum* has recently been redescribed and figured by Foerste (1928, pp. 261-262, pl. 40, fig. 2) as "*Orthoceras desideratum* (Billings)." It bears so little resemblance to typical *Glossoceras*, that one can not help but wonder why Billings referred it to this genus. Also, it is extremely doubtful if the single specimen from an unknown horizon in southeastern Poland (Łanowce) that Siemiradzki²⁵ described and figured as *Glossoceras carinatum* (the specific name is ascribed to Alth, who apparently used it in unpublished manuscript) actually represents this genus. That specimen is a small fragment which apparently was interpreted as representing the extreme adoral end of the living chamber, and the only published description of it is so incomplete as to be of little value.

Lindström has suggested (p. 33) that this genus can be differentiated from typical *Ascoceras* by the fact that the adoral dorsal portion of its phragmacone continues to increase in dorso-ventral thickness adorally, whereas in *Ascoceras* the adoral segments of the phragmacone are relatively small. This is true in the examples cited by Lindström, but there are so many exceptions to it, that the generalization is of little value. As a matter of fact, the conchs of members of this genus are very similar to those of some of the representatives of *Ascoceras* and can be distinguished from them only by their lobed apertures. The genus can be differentiated from other similar genera by the criteria mentioned at the close of the discussion of the genus *Ascoceras*.

²⁵ Siemiradzki, Jos. von, Die paläozoischen Gebilde Podoliens: Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, vol. 13, pp. 203, 227, pl. 18 (4), figs. 7a, b, c, 1905.

Genus CHOANOCERAS Lindström 1890

[= *Choaniceras* Lindström 1888, *nomen nudum*]²⁶ .

Plate IX, Figs. 1-9

This genus was established by Lindström to include a unique species, *Choanoceras mulabile* Lindström of the uppermost formation (Lindström's "stratum h") of the upper Middle Silurian of Gotland, and as far as the writer has been able to learn no other representative of it has been recorded since.²⁷ The genotype has been exceedingly well described by Lindström (pp. 35-37), but in as much as his monograph is not readily available to many paleontologists, the following concise description may prove of interest.

The conch is long and narrow and, being circular in cross section and only very gradually expanded orad, is essentially cylindrical in shape, but it is gently curved exogastrically. The earlier stages of the phragmacone are not known, and apparently they were broken off during the life of the individual; the conch of mature specimens consists of the adoral five camerae of the phragmacone and the living chamber. In these specimens the living chamber occupies at least nine-tenths of the remaining portion of the conch. The extreme adoral portion of the conch has never been observed, but as none of the known representatives is contracted adorally, the aperture probably was not constricted and was circular in outline. The surface of the test is marked by fine sinuous longitudinal lines and that of some internal molds by "microscopically small elevated points," which Lindström regarded as "belonging to an interior stratum of the shell."

The sutures are all parallel and nearly straight but are slightly inclined to the long axis of the conch; they slope orad from the venter. The septa are asymmetrically subconical in shape, and in mature specimens the adoral three are not complete as they unite and then coalesce with the preceding septum slightly ventrad of the siphuncle and become distinct from it again only in the extreme ventral part of the conch; this leaves a large elliptical lacuna in the ventral half of each septum, that is comparable to the much larger lacuna in the dorsal portion of the adoral septa of the ascoceratoids. In immature specimens only the adoral three cam-

²⁶ Lindström, G., List of fossil faunas of Sweden, p. 7. [Not seen by the writer]

²⁷ Hyatt (1900, p. 515) and Broili (1924, p. 524) list this genus as occurring in both the Ordovician and the Silurian, but the writer has not been able to locate the basis for this statement.

erae of the phragmacone are retained and all of the septa are complete, but as the individuals near maturity, the number of camerae that are retained is increased, the septa become more strongly asymmetrical and the distance between them is decreased, and the adoral septa coalesce in the ventral half of the conch as explained above.

The siphuncle is small at its passage through the septa but the septal necks are strongly recurved and the segments of the siphuncle are greatly expanded transversely within the camerae. The shape of the connecting rings varies with the stage of growth of the individual; in the smallest specimen known they are subcylindrical, but in somewhat larger specimens they are relatively shorter and are subspherical, whereas in mature specimens they are asymmetrically subnummuloidal.

It is perhaps very significant that in mature specimens a peculiar deposit, called a "spur" by Lindström, is formed on the inside of the septal necks. This deposit nearly closes the septal aperture, and Lindström detected a small conical plug that sealed the remaining opening in the septum of truncation.

The relationship of this genus to the genera described above is more or less of an open problem. The variation in the shape of the siphuncular segments in the different parts of the phragmacone, the coalescing of the adoral septa, and the truncation of the earlier stages of the phragmacone, all indicate a relationship to the ascoceratoids. However, that relationship can not be very close for the siphuncle of this genus is essentially central in position, the change in the shape of its segments is gradual, as far as is now known all of the septal necks are strongly recurved, the septa coalesce on the ventral side of the conch instead of on the dorsal (or, as is possible but very improbable, the conch is curved endogastrically rather than exogastrically), the septa are much more strongly convex and do not form long deep dorsal saddles, and the adoral part of the conch is not contracted so that the aperture apparently remained wide open throughout the life of the individual. It is probable that the shape of the aperture has been overemphasized in the classification of the nautiloids, for it probably depends somewhat upon feeding habits, i.e., those forms with strongly constricted apertures must have fed on microscopic food; nevertheless, the fact that in this genus the aperture is so markedly dif-

ferent from those of all of the other forms discussed above, serves to emphasize lack of close relationship.

These facts, taken together, have led the writer to the conclusion that this genus must represent a stock that differentiated from the main stock of the Mixochoanites early in the Ordovician, and that we have not discovered earlier representatives of the group as yet. It is therefore believed that *Choanoceras* should be regarded as an outlying member of the Mixochoanites, but it certainly should not be placed in the same family with any of the other known forms.

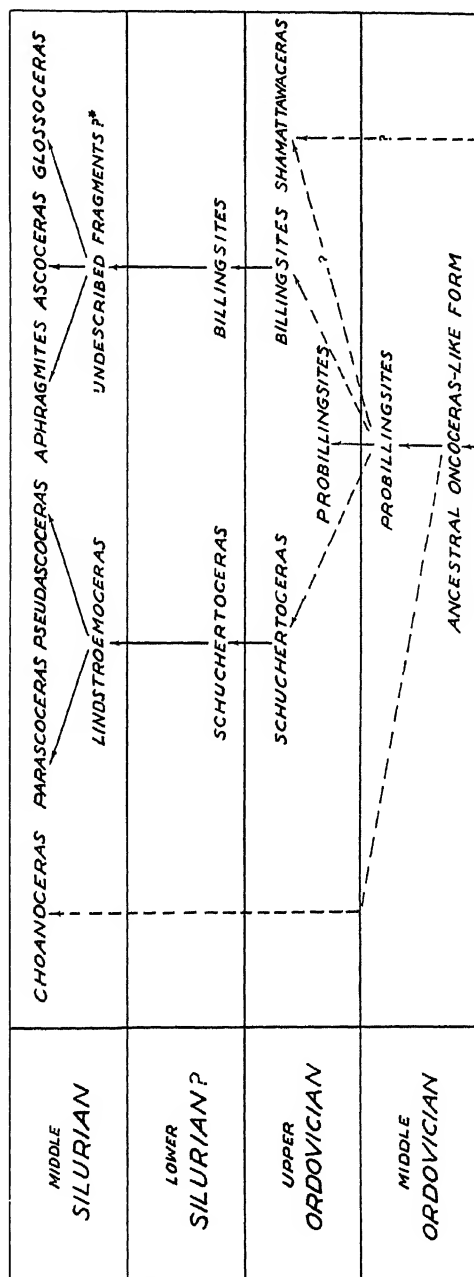
THE EVOLUTION OF THE MIXOCHOANITES

With one or two possible exceptions, the genera discussed above constitute a group of nautiloids that are closely related and are quite distinct from all of the other multitudinous forms known. The most significant feature that they share in common, and is not known to occur in any of the other groups of nautiloids, is the marked change in the nature of their siphuncle as they near maturity, i.e., a change from an orthochoanitic to a cyrtochoanitic structure. This, taken together with such other abnormal features as the unusual shape of their conchs, the universal truncation of the earlier stages of their phragmacones, and the peculiar shape and the coalescing of their adoral septa, makes it obvious that these forms constitute a distinct group, for which the name Mixochoanites of Hyatt is particularly applicable.

This group apparently originated early in the Ordovician²⁸ and can be definitely recognized by the middle of that period in *Probillingsites*. That genus obviously developed out of an *Oncoceras*-like form, but the writer has not been able to locate a definite ancestor of it. The available evidence seems to indicate that *Probillingsites*, or its progenitor, gave rise to two stocks which can be differentiated by the presence or absence of a so-called "basal" septum. These stocks became distinct at least by Upper Ordovician times and developed along closely parallel lines to the close of the Middle Silurian. In the upper Middle Silurian both apparently reached a climax, for they suddenly branched out into a variety of forms and then became extinct. What appears to be the culmination of a third stock is to be seen in *Choanoceras* of the upper Middle Silurian, but unfortunately the earlier stages of that stock are not known. Apparently it differentiated from the main stock of the Mixochoanites early in the Ordovician, and we have not found any but its ultimate stage as yet.

The general scheme of the evolution of this group as conceived by the writer is obvious from the accompanying diagram, and few

²⁸ The specimens from the Ozarkian (Oncota dolomite) of Dresbach, Minnesota, that were described by F. W. Sandeson (Minnesota Acad. Nat. Sci. Bull., vol. 4, no. 1, p. 102, 1896) under the name "*Ascoceras gibberosum*" are stated by Foerste (1924, p. 217) on the authority of E. O. Ulrich to represent "a new genus of *Chiton*, related to *Priscochiton*, now under investigation."



PHYLOGENIC TABLE OF THE MIXOCHOANITES

* Indeterminable fragments of ascoceratoids in the oolite of Bursvik and the limestone of Östergarn, Gotland, (both formations are of lower Middle Silurian age) may represent an intermediate stage between *Billingsites* of the Upper Ordovician and probably the Lower Silurian and *Ascoerzas* s. s., *Aphragmites*, and *Glossoceras* of the upper Middle Silurian—no description of them has been published.

supplementary remarks are necessary. The genus *Shamattawaceras* is so incompletely known that it is by no means certain that it should be included in the Mixochoanites, but because of the general similarity of the form of its conch and its sutures to those of *Probillingsites*, it is tentatively associated with that genus.

This diagram serves also to indicate the chronological distribution of the various genera concerned, but it does not present their geographical distribution. The available evidence seems to indicate that this group, the Mixochoanites, originated early in the Middle Ordovician in an epicontinental sea in the interior of North America and slowly migrated from there northeastward, where it apparently underwent further development in an arctic or subarctic sea, probably a branch of the northern Atlantic. In the latter part of the Upper Ordovician it then spread southward into North America, where it is exceedingly widespread, and into northwestern Europe, where it may have lingered during the early part of the Lower Silurian²⁹. During the first half of the Middle Silurian, as in the Lower Silurian, it is not known to have been represented in North America and apparently was only sparingly represented in northwestern Europe (Gotland), but in the last half of that epoch it again entered the interior of North America from the Arctic, and was present in northwestern Europe as well, where it was more widespread than ever before and was abundantly represented in the shallow seas that transgressed Gotland, Bohemia, and England. With the retreat of the seas at or near the close of the Middle Silurian the Mixochoanites as a group became extinct.

It is interesting to note the changes that took place in this group during its development and to speculate as to their causes. Living nautiloids swim backward by jet propulsion, and therefore it is logical to assume that the mixochoanites did likewise. Long, slender shells would be a serious handicap to such a mode of locomotion, and particularly so when they were slightly curved—in fact one can not help but wonder how many of the cyrtoconic forms controlled the direction of their progression during backward propulsion. Therefore, it must have been distinctly advantageous to

²⁹ It should perhaps be mentioned in this connection that the occurrence of such transitional types as *Billingsites* and *Schuchertoceras* in the Richmond of North America, the Kallholm or Upper Leptaena limestone of Sweden, the Gastropod limestone of Norway, and the Lyckholm of Estonia, indicates that those deposits were all formed at approximately the same time in one continuous sea.

break off the earlier stages of the phragmacone and thus remove much of the impediment to rapid and straight progression. Such truncation, however, necessitated the development of a few large camerae or gas chambers next to the living chamber to serve as buoys, and this will perhaps account for the globular form assumed by the early mixochoanites. Utopia was not attained, however, by these early forms, for they apparently had two serious handicaps: first, when the animal came to rest its conch must naturally have assumed a vertical position with the aperture down (cf. modern *Spirula*); and, second, its globular form must have retarded its passage through the water. The first of these handicaps was surmounted by the development of long, deep dorsal saddles in the adoral septa (the ones that were retained after truncation), so that the phragmacone (buoy) was extended all along the dorsal part of the conch and the weight of the animal's body was distributed all along the ventral. The second handicap was overcome by what superficially appears to be a reversal in evolution in that the conch tended to become long and narrow again, but this time it assumed a spindle-like or fusiform shape, which is particularly advantageous for subaqueous locomotion.

The curious thing is that in this group, as in many other groups of animals, extinction followed close upon the heels of perfection, and the writer is as much at a loss to explain this phenomenon adequately as his predecessors have been. Possibly it was due to a lack of weeding out of the unfit and therefore a weakening of the race as a whole so that it was not able to cope with some new environmental change or enemy; or possibly the group simply perished from racial old age. It is of course true that at the close of the Middle Silurian the habitat of these forms, the shallow epicontinental seas, was greatly restricted, but it is hardly probable that it was extinguished for many other forms requiring a similar habitat continued on into the succeeding epoch.

THE CLASSIFICATION OF THE MIXOCHOANITES

The characters which differentiate this group from the rest of the nautiloids are given above, and in the writer's opinion the group is quite as distinct as it was regarded by Barrande and Hyatt and should therefore be considered as representing one of the major divisions of the order Nautiloidea and be accorded the rank of a suborder. Hyatt, the only paleontologist who has so far attempted to subdivide the group into units larger than genera, recognized two families, but in as much as one of them included only *Mesoceras*, which apparently should be excluded from the suborder, and *Billingsites*, which is in the direct line of the evolution of *Ascoceras*, the type of the other family, his subdivisions are no longer tenable.

If the evolution postulated above is correct, three logical subdivisions of this group should be recognized. The two main stocks apparently differentiated from *Probillingsites* or its progenitor before the Upper Ordovician and can be followed almost continuously to the close of the Middle Silurian, when both became extinct. One of these, which is characterized by the absence of a so-called basal septum and, in some cases, by the possession of a relatively large number of sigmoidal septa (in one form as many as twelve) in the adoral part of the conch, can be definitely recognized in *Billingsites* and followed through to its culmination in *Ascoceras*, *Aphragmites*, and *Glossoceras*. The other stock, which is characterized by the possession of a basal septum, or vestiges of it³⁰, and a relatively small number of sigmoidal septa (never more than four or five) in the adoral part of the conch, can be recognized in *Schuchertoceras* and followed through *Lindstroemoceras* to its culmination in *Parascoceras* and *Pseudascoceras*. The third stock, which apparently culminated in *Choanoceras*, probably originated early in the Ordovician, but at present we know it from only its ultimate stage. This stock can be differentiated from the other two by the fact that its siphuncle is essentially central in position, the change in the shape of its siphuncular segments is

³⁰ In at least two representatives of this family, *Schuchertoceras* and *Pseudascoceras*, the first septum formed oral of the septum of truncation apparently was resorbed before the succeeding septum was secreted.

gradual, all of its septal necks (as far as is now known) are strongly recurved, its septa coalesce on the ventral (rather than the dorsal) side of its conch and do not form long, deep dorsal saddles, and the adoral part of its conch is not contracted and its aperture apparently was wide open throughout the life of the individual.

The writer would therefore recognize three families of the Mixochoanites; one of these has been aptly named Ascoceratidae by Barrande, and it is here proposed to call the second Schuchertoceratidae and third Choanoceratidae. All of the genera known fall logically into these three families, with the possible exception of *Probillingsites* and, along with it, *Shamattawaceras*. Both of these genera are so incompletely known that it is not now possible to determine whether they should be placed in the Ascoceratidae or the Schuchertoceratidae, or whether *Probillingsites* should be regarded as the ancestor of both of those groups. In view of the equivocal nature of the available evidence, the writer has thought it best to place *Probillingsites* tentatively in the Ascoceratidae, as that group was far more abundant than the other and apparently should be regarded as constituting the main stem of the Mixochoanites; the other stocks then should be considered offshoots of it. *Shamattawaceras* is also tentatively assigned to the Ascoceratidae as apparently it should be associated with *Probillingsites*.

SUMMARY

To summarize the above statements, it can be stated that the Mixochoanites, which are confined to the Ordovician and Silurian of central and northeastern North America and northwestern Europe, constitute a natural group of nautiloids that is distinct enough to deserve the rank of a separate suborder; that certain of the genera, viz., *Volborthella*, *Ophidioceras*, and *Mesoceras*, that have been included in that group have little or no relation to it and should be excluded from it; and that the number of subdivisions, both genera and families, of the group that have been recognized previously is not as large as the diversity of its forms justifies. The following classification of the group is therefore proposed:

Suborder MIXOCHOANITES Hyatt

Family ASCOCERATIDAE Barrande

Genus *Ascoceras* Barrande

Genus *Aphragmites* Barrande

Genus *Glossoceras* Barrande

Genus *Billingsites* Hyatt

Genus *Probillingistes* Foerste

Genus *Shamattawaceras* Foerste and Savage

Family SCHUCHERTOCERATIDAE Miller, n. fam.

Genus *Pseudascoceras* Miller, n. gen.

Genus *Parascoceras* Miller, n. gen.

Genus *Lindstroemoceras* Miller, n. gen.

Genus *Schuchertoceras* Miller, n. gen.

Family CHOANOCERATIDAE Miller, n. fam.

Genus *Choanoceras* Lindström

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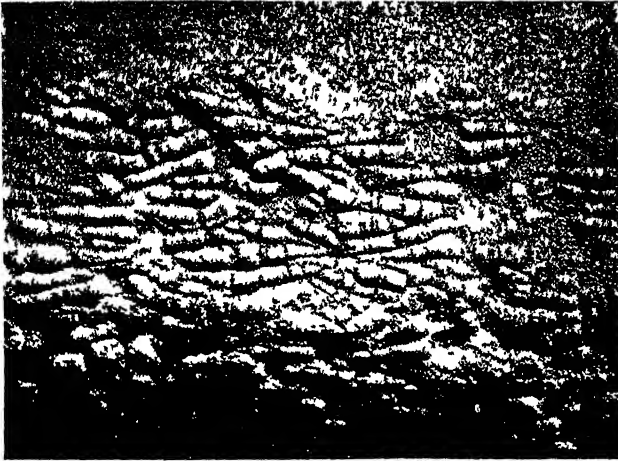
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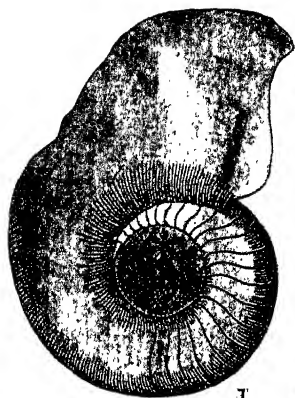
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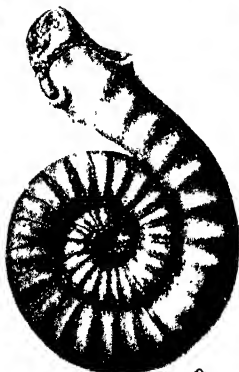
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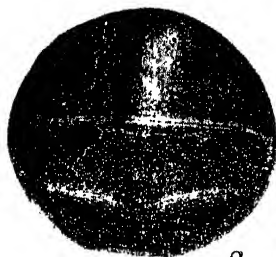
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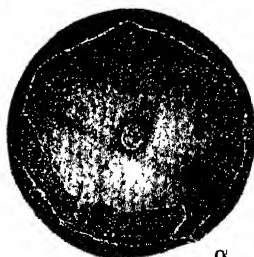
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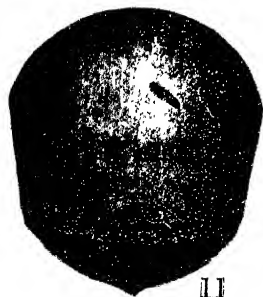
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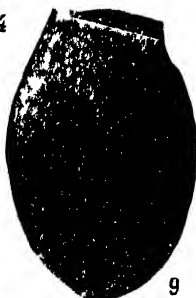


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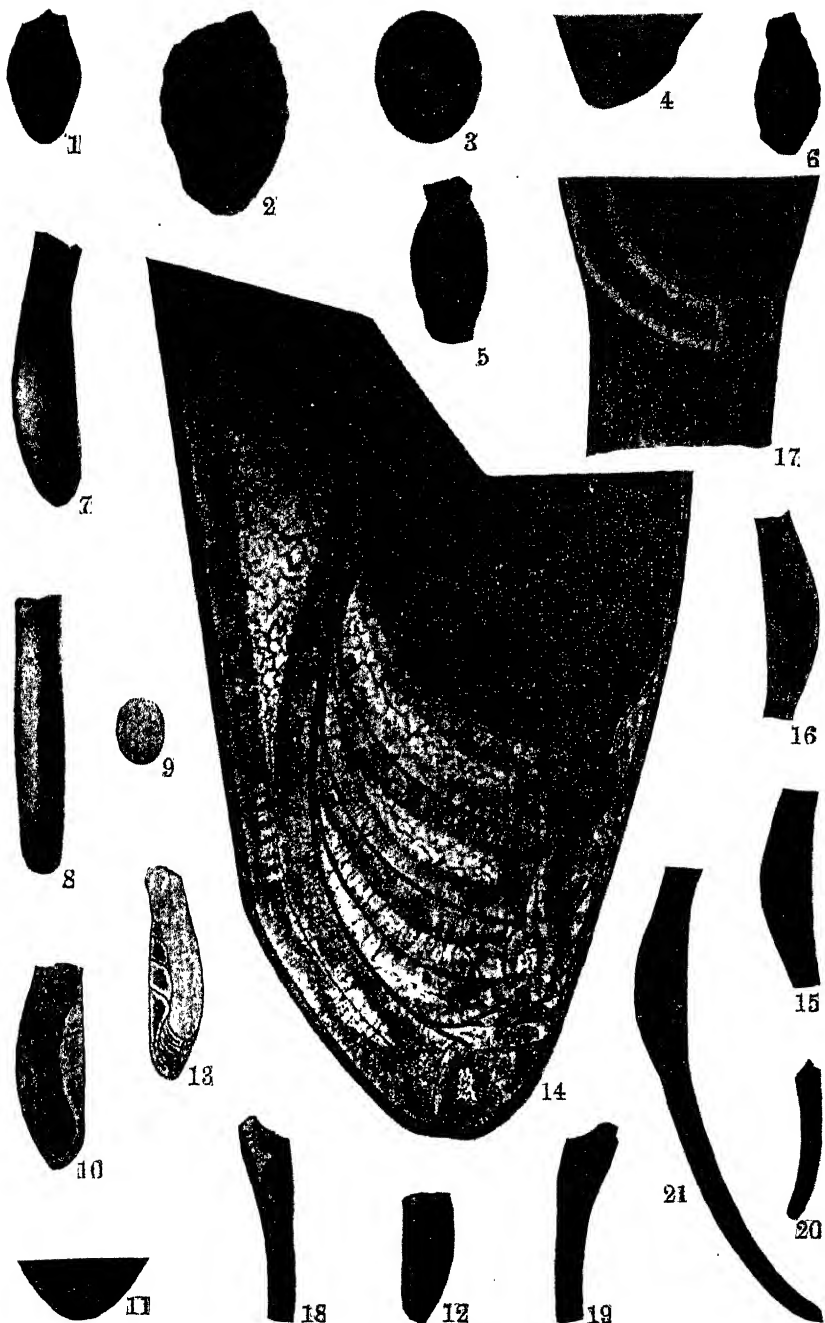


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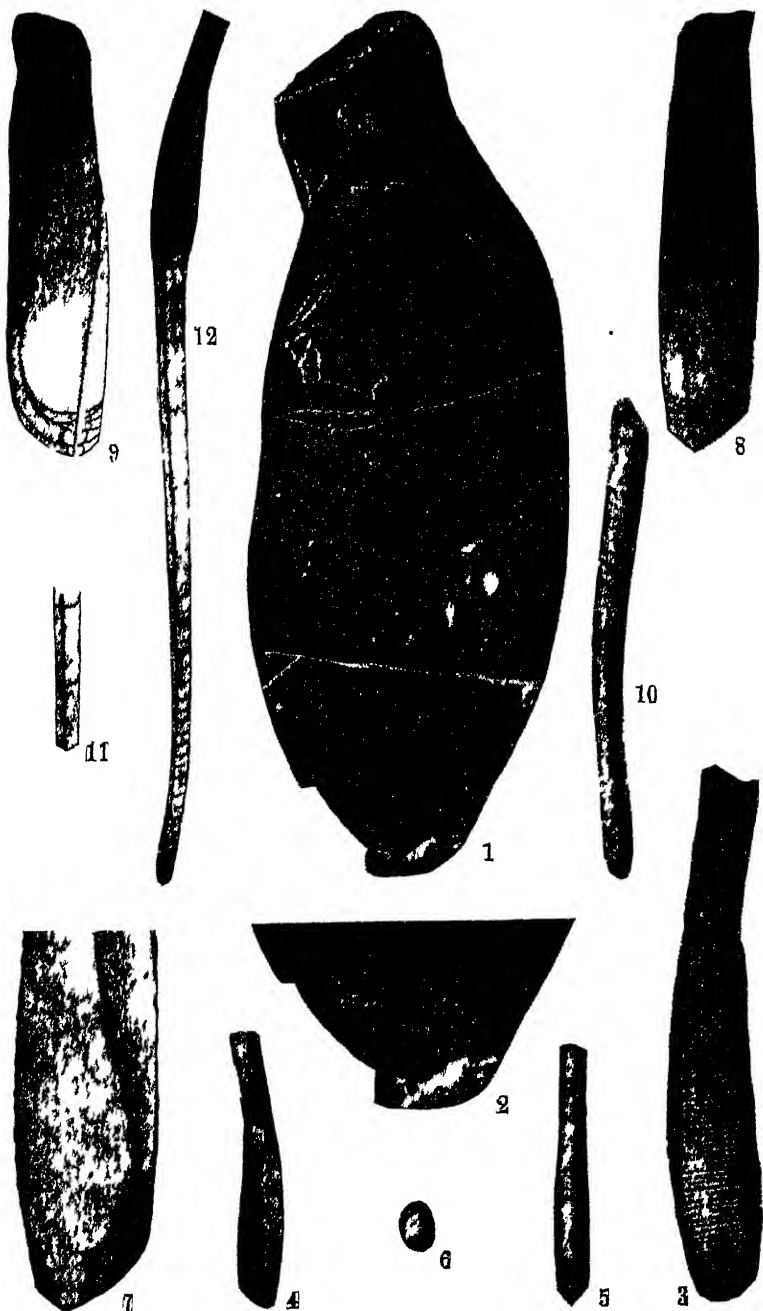


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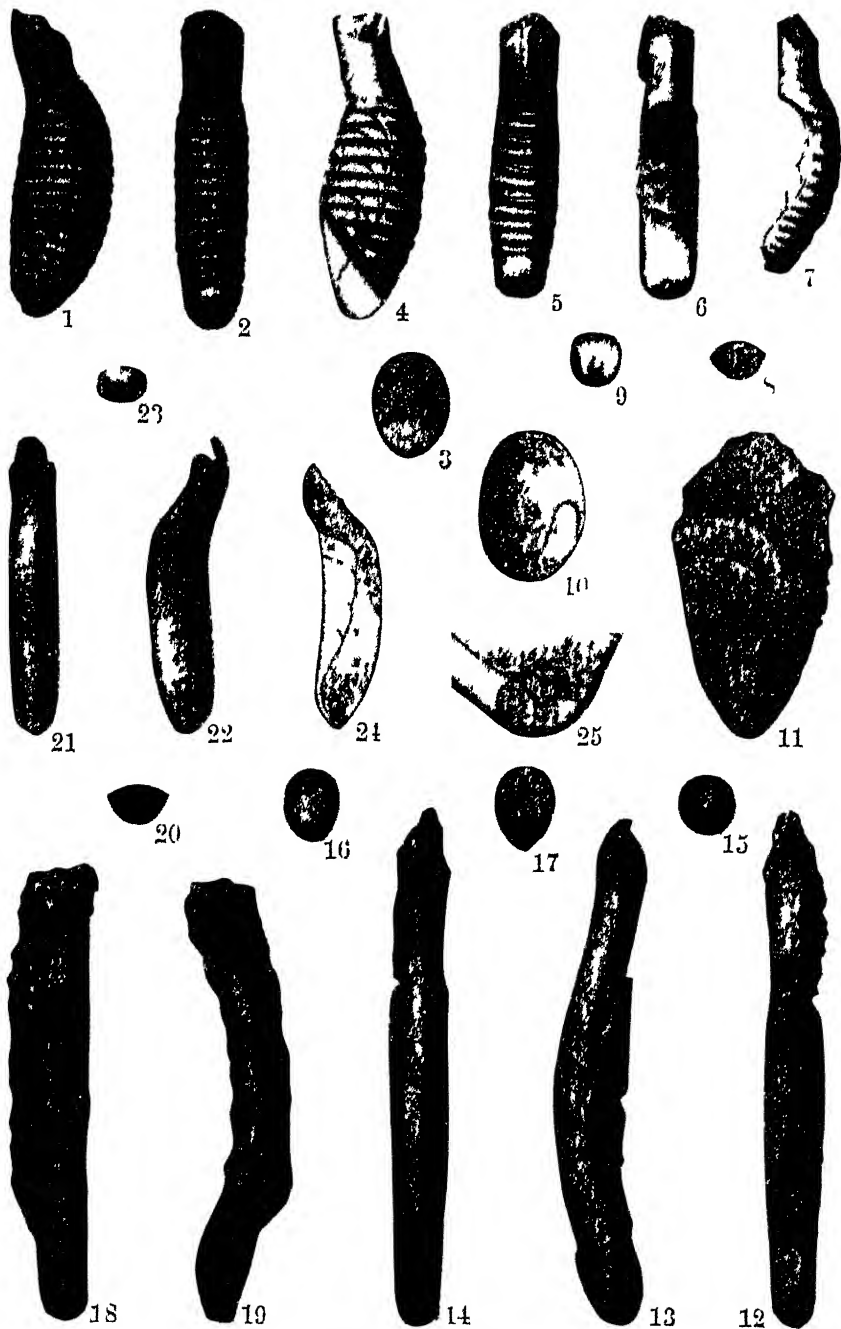


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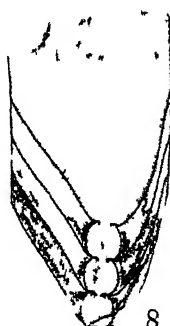
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THE DEVELOPMENT OF FOLIAGE LEAVES

by

BERYL TAYLOR MOUNTS

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1932

THE DEVELOPMENT OF FOLIAGE LEAVES

INTRODUCTION

BERYL TAYLOR MOUNTS

This paper presents the results of a study of leaf development in two mesophytic plants, *Vitis vulpina* L. and *Catalpa bignonioides* Walt. The investigation was undertaken with the hope of gaining additional information on the development of the islet tissue which lies between the veinlets and constitutes the main body of the leaf. *Vitis* was chosen as one type because new leaves are produced throughout the summer months. *Catalpa* on the other hand has limited leaf development, normally producing but one set of leaves each year. Mesophytic plants were selected since they are related to intermediate habitats and their leaves may be sectioned readily. Facts concerning mesophytic leaf development establish a basis for comparisons with hydrophytic, xerophytic, or other types.

The leaf, which is perhaps the most important vegetative organ of the plant, is a highly specialized structure. Its work involves a large superficial area, multitudinous openings for gaseous exchange, an extensive series of internal air spaces, and a ramifying system of veins and veinlets for conduction and support. The whole structure is denied adequate protection since it cannot function with other than a transparent covering. Such an organ encounters numerous problems in the performance of its major functions as it must expose extensive areas to external conditions while denied the protection of other plant parts.

Detailed studies of leaf development are necessary to round out our knowledge of the higher plants. Information on the normal course of leaf development affords a basis for interpretation of abnormal growths, for the study of changes due to environmental conditions, and may possibly strengthen conclusions regarding phylogeny. For practical workers also it is important to know at what stage the stomata become functional and the structure of the leaf at varying ages. Especially helpful is such information to all botanical workers if it enable one to correlate internal structure

and developmental stages with obvious external changes or characters of the leaf.

Papers concerned with leaf development while numerous have dealt chiefly with their external aspects. Such of the developmental investigations as involved internal structure have been concerned mainly with the venation or with the vascular system in its relation to leaf form. Deinema (2) expressed the view that the mid-vein of the leaf is laid down first, then the lateral veins, and that the mature shape and venation of the leaf depends on whether elongation of the cells is greater in the longitudinal or in the transverse direction. Freundlich (4) stated that the mid-vein appears first; that there are lateral veins of the first, second and third order, and that the kind of vascular development is dependent upon the position of the meristem. Many papers have dealt with the structure of the mature leaf and especially with the morphology of the leaf in relation to its habitat but have not discussed the development of these organs. Goebel (5) who reviewed the history of the study of leaf development and discussed the growth of the leaf as a whole states "We may say in general that parts which have earlier functions to perform appear earlier." Development of the islet tissues has received relatively little attention with modern methods of study and interpretation.¹

¹ Foster's paper (Foster, Adriance S. Investigations on the morphology and comparative history of development of foliar organs. I. The foliage leaves and cataphyllary structures in horsechestnut (*Aesculus Hippocastanum* L.) Am. Jour. Bot. 16:441-501. 1929), published since this study was begun, discusses certain phases of foliar development. The bud scales of *Vitis* are found in the winter bud only, are without chlorophyll and not persistent, so are not comparable to the cataphylls of *Aesculus*. His discussion of the development of the blade is chiefly on the order in which the leaflets appear. *Vitis* and *Catalpa* with their simple blades do not have separate leaflets but it is interesting that in both the apical tip of the leaf develops first, paralleling the early growth of the median leaflet in *Aesculus*. Foster does not follow the development of the islet tissue.

MATERIAL AND METHODS

The investigation of *Vitis* was begun in June and series of buds and leaves in various stages were collected at intervals during the summer. During the winter buds were collected periodically and from twigs kept in the laboratory buds were removed and preserved as they began to swell or open. Collections were continued through the following spring and summer. Buds of *Catalpa* were taken in February and collections of buds and leaves in various stages were continued until June.

For microscopic study material, killed in 1% chromo-acetic and imbedded in paraffin, was cut 5-20 μ in thickness. In addition to the usual transverse sections others were cut parallel with the surface of the leaf. The latter proved especially helpful in studying the palisade tissue and the relations of interior cells to epidermal layers. Longitudinal sections of buds of various ages were necessary for the earlier stages of leaf development. Several stains were used but Safranin-Haematoxylin proved the most useful in this study. All drawings from sections were made by means of a Spencer drawing apparatus; these preliminary drawings were completed in detail, cell by cell, with the compound microscope under oil immersion lens.

In determining rate of growth certain tagged leaves were measured daily. The first series of measurements, on very small leaves, involved length only, but later series included both length and breadth. In determining distribution of growth for leaves over 3 cm. in length a special rubber stamp was devised for marking the leaf surface. This stamp had a ruled surface 8 x 8 cm. divided into 5 mm. squares, and was mounted on a wooden block having a thick rubber pad between the block and the stamping surface. A soft support, slit at one side to receive the petiole, was placed under a leaf while the upper surface was being marked by the stamp. After considerable experiment a mixture of three parts India ink and one part glycerine was found satisfactory for marking leaves. This medium did not harm the leaves nor was it washed off by the heaviest rains.

Permanent records of the further growth of leaves thus marked

were made in the following manner. Unexposed and undeveloped photographic dry plates were fixed, washed and dried. A plate was held firmly over a leaf, supported by a pad below, and the ink lines of the stamped area were traced with a sharp steel point in the transparent film on the plate. In this way a series of records could be made during the expansion of a leaf blade, showing the relative growth of all its parts. The lines on the plate were then intensified with India ink and the plates numbered and filed for reference.

LEAF DEVELOPMENT

I. *Vitis vulpina* L. (Wild grape)

General description of the mature leaf

The mature leaf of *Vitis* may be 20 x 22 cm. but the average of those studied was about 11 x 12 cm. This leaf is usually three-lobed, with broad rounded or truncate sinuses and large acute or acuminate teeth (fig. 6). Rarely there are five instead of three lobes, and in some the margin is not lobed at all. The mature leaf of *Vitis* averages 144 μ in thickness, the upper epidermis making up about 10% of this total, the palisade 35%, the spongy mesophyll 46% and the lower epidermis 9%. The upper epidermal cells are relatively large, averaging 32 μ in surface width. The cells of the lower epidermis are somewhat smaller, about 26 μ , their outer walls being less convex and less heavily cutinized than those of the upper epidermis. Stomata are confined strictly to the lower epidermis, (fig. 8).

The palisade cells, consisting of one row, are slender, usually slightly bell-topped, average about 9.6 μ in diameter near the middle and 51 μ in length. They do not form a compact tissue as there are intercellular spaces about each cell. Sections cut parallel to the surface disclose certain relations not evident in the transverse view. The palisade cells, seen thus in cross section are approximately circular in outline except in the junction plane with the upper epidermis. They are always at least partly free from lateral contacts (compare figs. 8 and 10).

The spongy mesophyll tissue consists originally of three cell layers, or rarely four, but at maturity these cells are loosely arranged and irregularly elongated in shape, usually with the longer axes parallel to the epidermis (fig. 8). In sections cut parallel to the surface the cells of the spongy mesophyll appear as a coarse network with lobes drawn out about the air spaces. These connected intercellular spaces occupy over 50% of the total mesophyll volume (fig. 8).

Early Development of the Leaf

The winter bud of *Vitis* is covered with three or four hard brown

scales and five or six densely hairy bracts. The most advanced foliage leaves in the winter bud are mere rudiments about 1 mm. long. The leaf starts as a lateral protuberance near the vegetative point (fig. 1). The stipules appear on its sides as two small papillae which grow more rapidly and are longer than the leaf itself until the blade is 2 mm. long, after which their growth is relatively slower, reaching their maturity by the time the leaf blade is about 8 mm. long. The stipules when mature are about 5 mm. long, 4-5 cells thick and contain no chlorophyll. They protect the young leaf in the bud and after the leaf emerges dry up and drop off.

The petiole is differentiated from the leaf base when the stipules are about 0.5 mm. long. The petiole remains short during the early development of the blade, beginning to elongate slowly when the lamina is about 3 mm. long. About the time the blade reaches 10 mm. in length the rate of elongation becomes rapid, forming a petiole one-half to two-thirds the length of the blade.

The apex of the blade early pushes out into a long rounded tip which lengthens rapidly and makes up about half the length of the blade when it is 2 mm. long. Small papillae appear along the lateral margin of the blade shortly after the tip begins to push out, the larger of these papillae forming the lateral lobes, the smaller ones the teeth (fig. 2). The meristematic tissue is differentiated into six (rarely seven) distinct layers before any specialization is evident. The cells of these layers at an early stage look alike and are distinguishable only by their position in cross section.

The mid-vein begins to differentiate in the second layer below the upper epidermis when the blade is about 1 mm. long. Its appearance is early indicated by a modified staining reaction and soon also by differences in the shape and arrangement of the cells. Annular markings on the tracheal tissue of the mid-vein are distinct by the time the blade reaches 2 mm. in length. The major lateral veins running to the margins appear next. While the development of the veins was not followed in detail in this study it should be noted here that new veinlets form from the uppermost mesophyll layer.

Differentiation of the Tissues of the Leaf Blade

This study has been concerned mainly with the development of the leaf tissue within the islet which is bordered laterally and supported by veinlets. These areas have most of the chlorophyll bear-

ing cells, stomata, and internal air spaces. In brief, the islet is the chief working portion of the leaf, all other parts being auxiliary to it.

The Epidermal Cells

The cells of the several layers begin to differentiate when the blade is 5-7 mm. long (fig. 5). The cuticle begins at this stage as a slight thickening on the outer wall. Mitoses in the upper epidermal cells continue, as evidenced by figures, until the blade is approximately 20 mm. long. All cells of this layer remain about the same size until division ceases but the lower epidermal cells, which have for a time a deeper staining reaction, continue dividing somewhat longer. By the time the blade is about 30 mm. long this deeper staining reaction is localized in scattered cells which are probably to form stomata.

Cell enlargement begins as mitoses cease. The epidermal cells through this phase increase little in thickness but their lateral expansion is marked. The cells of the upper epidermis at the time enlargement begins average $7\ \mu$ in width; in the mature leaf they average $32\ \mu$, an increase of 357% in diameter, making 21 times the original area. In the mature leaf the lower epidermal cells average $26\ \mu$ across, an increase of 270% in diameter or about 14 times in area. As stated above mitoses continue longer in the lower epidermal layer, thus there are more cells in a given area of this tissue than in the upper epidermis.

The earlier stomata make their appearance when the blade is some 14 mm. long. Some stomata begin to open when the blade is 35-40 mm. long but all do not become functional at one time. A leaf 50-60 mm. has functional stomata separated by only a few intervening cells from guard cells in the initial stages of development (fig. 7).

The Palisade Layer

The cells of the palisade as differentiation begins, appear, in transverse section, tightly packed together and slightly longer than in other zones of the leaf, averaging approximately $15\ \mu$ in length. Cell division, however, is here continued longer than in the contiguous upper epidermis, for while at this stage the palisade and upper epidermal cells are about equal in number in a given area, at maturity there are approximately five palisade cells which in-

crease 240% in length but show only moderate change in diameter. Their average width at the conclusion of cell division in the epidermis is 7 μ and at maturity 9.6 μ in the middle plane and 11 μ at the upper end where they meet the epidermis. It should be noted here that these two adjacent layers with cells of equal size, enlarge in different degrees. While the upper epidermal cells enlarged to approximately 21 times their original area the adjacent palisade cells in the same leaf area have enlarged, after allowing for increase in number to a total cell-area of less than ten times that of early differentiation stage. The shape of the palisade cells, seen in cross section changes, from the initial polygonal outline to approximately circular form except at the upper junction plane where they keep much of their angular shape (compare figs. 4, 9, and 10). This change of shape is correlated with the development of the intercellular spaces among the palisade cells, which in turn is related to the unequal expansion of epidermis and palisade.

The Mesophyll Tissue

The three layers of cells which give rise to the spongy mesophyll are somewhat less uniform in size and stain more deeply than the palisade (fig. 5). The uppermost layer of the mesophyll tissue is slightly different from the other layers in having smaller cells and staining more deeply. This is doubtless related to the development of the vascular system of the leaf since the veinlets originate from this layer and mitoses continue here after cell division has ceased in all other layers of the islet.

During the differentiation of the mesophyll its cells not only enlarge but change their relations. At the time cell division ceases their longer dimension is perpendicular to the surface of the leaf. As the blade enlarges the cells are partly separated from one another, and from the epidermis in part, leaving intercellular spaces, the larger of these appearing above the differentiating stomata (fig. 12). The mesophyll cells at maturity are lobed and irregularly stretched out with their longer axes in most cases parallel to the epidermis, thus forming a coarse net-work (fig. 11). In the transverse section these relations and connections are not apparent (fig. 8).

Intercellular spaces occur throughout the interior of the leaf. They were first clearly noted as tiny spaces between rounded corners of adjacent cells above the developing stomata when the blade

was about 20 mm. long. At about the same time gaps appear between other mesophyll cells and then among palisade cells. As the leaf expands these spaces are enlarged, uniting with other spaces, and forming a system which ramifies throughout the islet area. At maturity probably more than half the internal volume of the *Vitis* leaf is air space. Every chlorophyll bearing cell of the leaf borders an intercellular space and is often laterally surrounded by these air chambers. The development of these spaces is undoubtedly related to the unequal expansion of the different tissues of the islet.

Rate of growth of the leaves

Spring leaves grew more slowly than those formed during the summer. The rate of expansion differed little for organs of approximately equal size under like conditions. The developing leaf passes over from the cell division stage to the cell enlargement phase when about 20 mm. long. Leaves 7-11 mm. long, measured for ten days during July, showed an average increase of 1.7 mm. per day. During April considerably larger leaves, entered upon the enlargement phase, showed an average daily gain in length of

TABLE 1. Rate of growth of spring leaves of *Vitis*.

No. of leaf	Date tagged	Initial length	Length at end of ten days	Average daily increase in length
1	April 24	25 mm.	30.6 mm.	0.56 mm.
2	" "	25 mm.	30.6 mm.	0.56 mm.
3	" "	27 mm.	32.2 mm.	0.52 mm.
4	" "	20 mm.	24.3 mm.	0.43 mm.
5	" "	39 mm.	44.7 mm.	0.57 mm.
Average for 5 leaves		27.2 mm.	32.48 mm.	0.52 mm.

TABLE 2. Rate of growth of summer leaves of *Vitis*.

No. of leaf	Date tagged	Initial length	Length at end of ten days	Average daily increase in length
101	June 26	33 mm.	70 mm.	3.7 mm.
102	" "	45 mm.	100 mm.	5.5 mm.
103	" "	53 mm.	143 mm.	9.0 mm.
104	" "	33 mm.	76 mm.	4.2 mm.
105	" "	35 mm.	65 mm.	3.0 mm.
106	" "	64 mm.	119 mm.	5.5 mm.
107	" "	72 mm.	109 mm.	3.7 mm.
108	" "	77 mm.	128 mm.	5.1 mm.
109	" "	63 mm.	96 mm.	3.3 mm.
110	" "	47 mm.	113 mm.	6.6 mm.
Average for ten leaves		52.2 mm.	101.9 mm.	4.97 mm.

only 0.52 mm. (Table 1). Slightly larger leaves made an average daily increase of 4.97 mm. through a ten day period beginning in late June (Table 2).

The distribution of growth in leaves of 30 mm. or more in length was studied from the series of records drawn on fixed photographic dry plates by the method described above. These records revealed a uniform distribution of growth and an absence of any special growing regions (fig. 6). The apical point, which earlier had grown so rapidly, enlarges but slightly during this phase. Near the mid-vein expansion in a transverse direction is frequently a little less than elsewhere but this difference is not marked. There are other minor variations here and there but these are slight and are not constant, so may be attributed to differences in surroundings. The expansion of the leaf in general is uniformly distributed throughout the blade.

II. *Catalpa bignonioides* Walt.

General description

Catalpa presents a very different habit since it is a tree instead of a vine. Only one set of leaves is regularly produced each year and these average several times larger than the *Vitis* leaf. *Catalpa* leaves are arranged alternately or in whorls of three, varying in length from 5-35 cm. The leaf has a cordate base and acuminate apex with smooth, unlobed margin. There are no stipules.

The foliage leaf of *Catalpa* varies considerably in structure. The thickness ranges from about 100 μ to 200 μ , depending chiefly on the width of the palisade tissue. Some leaves show two layers of regular palisade and a third layer of elongated cells which appears intermediate between palisade and spongy mesophyll. Other *Catalpa*

TABLE 3. A comparison of the mature *Catalpa* leaf with that of *Vitis*. These figures except where maximum and minimum are stated are averages of several measurements.

	<i>Vitis</i>	<i>Catalpa</i>
Thickness of leaf	144 μ	100-200 μ
Thickness of upper epidermis	15 μ	17 μ
Thickness of palisade layer	51 μ	40-100 μ
Thickness of mesophyll	65 μ	26-66 μ
Thickness of lower epidermis	13 μ	17 μ
Diameter of upper epidermal cells	32 μ	25.8 μ
Diameter of palisade cells at junction plane	11 μ	11.4 μ
Diameter of palisade cells at middle plane	9.6 μ	10 μ

leaves have only one complete palisade layer with an additional modified layer (fig. 18).

Development of the Blade

The *Catalpa* leaf follows the same general course of development as *Vitis*. The primordia push out as lateral protuberances from the vegetative point and differentiate into leaf base, petiole and blade when the leaf is approximately 0.5 mm. long. The meristematic layers are clearly differentiated by the time the blade is 1.5 mm. long. The number varies; some leaves show six layers of cells, others only five (figs. 14, 15). Veins make their appearance when the blade is 2-3 mm. in length, developing from the uppermost mesophyll layer as in *Vitis*. The size of the leaf at the time cell division ceases varies considerably in different leaves on the same shoot and is related to the dimensions of the leaves at maturity. In some there is no division after a length of 15 mm. is reached as evidenced by changes in the cells of the various layers; in others division continues until the blade is 60 mm. long; the latter resulting of course in a much larger leaf. The epidermal cells when they cease division, average $7.9\ \mu$ in surface width; at maturity they average $25.8\ \mu$, an increase of 226% in width or ten times in area; that is, at maturity each is about 11 times its original area.

The mature palisade differs somewhat from *Vitis*. Originally there is but one layer of palisade tissue, but periclinal divisions frequently occur, giving rise to a double or even triple palisade layer. There appear to be two anticlinal divisions of the palisade cells after the upper epidermal cells cease to divide. When the latter begin their expansion, the number of palisade and epidermal cells in a given area is equal; at maturity the ratio is 4 to 1 (fig. 21). The palisade cells average $7.1\ \mu$ in diameter when they cease dividing, at maturity they average $11.4\ \mu$ at the junction plane with the upper epidermis and $10\ \mu$ at the middle plane, an increase of 184.5% in diameter giving approximately eight times the total cross sectional area at the middle plane (fig. 19). Meanwhile the contiguous epidermis had expanded to eleven times its original area.

The mesophyll tissue in some leaves is differentiated as two layers, in others as three layers (figs. 14-15). Mitoses cease at about the same time as in the epidermal layers. In maturity the mesophyll

cells are less changed than in *Vitis* and about half of them have their long axis parallel to the epidermis (figs. 18, 20).

Measurements on the rate and distribution of growth showed an average increase in length of 9 mm. per day through a ten day period, for leaves that were approximately 40 mm. long. Growth during this period of expansion is uniformly distributed throughout the area of the blade.

Discussion

The results of this investigation are difficult of correlation or comparison with the work of earlier botanists for those workers were concerned mainly with the external aspects of leaf development. Such as made structural study of development were interested in veins rather than in islet tissue. Yet many of their general findings harmonize with the detailed development of *Vitis* and *Catalpa* as worked out in this paper.

The appearance of the mid-vein followed by the major lateral veins while the leaf is still in the bud supports the view of Deinema (2), Freundlich (4) and others who state that these veins arise very early.

Goebel's (5) statement that parts which function first mature earlier finds support by several points in the development of these leaves: (a) in *Vitis* the early appearance and growth of the stipules which function as a protection to the young leaf in the bud, (b) the delayed growth of the petiole which keeps the young blade in the bud and later by rapid elongation brings it out into more favorable light relations when the leaf is ready for photosynthesis, (c) the appearance of the intercellular spaces first above the differentiating stomata.

The intercellular spaces of higher plants are analogous to the air chambers of lower plants. The origin of the air chambers in the liverworts has been studied by a number of botanists. Hill (6), Evans (3) and Pietsch (8) stated that the air spaces are schizogenous in origin. Hirsh (7) argues that in the Ricciaceae there are two methods of origin for the air spaces:—by internal cleavage resulting in the formation of broad, irregular chambers separated by plates of green tissue one layer of cells thick; by the upward growth of filaments at right angles to the surface of the thallus, resulting in the formation of narrow elongated air chambers. This

latter process has of course no possible equivalent in the foliage leaf of higher plants.

Barnes and Land (1) in their paper on the origin of air chambers in the Marchantiales state, "In as much as new cells are produced by division, and the partitioning wall is a joint product of the two severed protoplasts, *a priori* reasoning leads to the hypothesis that the intercellular spaces arise by secondary splitting of the membrane, on account of unequal growth and turgor." They cite no figure of air spaces originating in this way in vascular plants, nor do they refer to any paper discussing such origin. Their own paper is limited to the Marchantiales. Smith (9) found that in *Isoetes* the air spaces formed by the disorganization of certain groups of cells. No disorganizing cells are visible at any stage in the leaf development of *Vitis* and *Catalpa*.

This study leads to the suggestion that these air spaces result in part from the unequal expansion of the epidermal layers and the interior tissues of the leaf. This strain must be marked especially in the lateral plane. Cells of the upper epidermis of *Vitis* when they cease division average $7\ \mu$ in diameter. The palisade cells at this stage are closely fitted together and have also an average diameter of about 7μ . From this stage forward the cells of the two layers do not enlarge at the same rate. At maturity the epidermal cells average $32\ \mu$, an increase of nearly twenty times in surface area. Cell division is continued somewhat longer in the palisade layer and at the end of the expansion phase there are about five palisade cells, averaging $9.6\ \mu$ in diameter at their mid-plane, to one epidermal cell. This results in an eight-fold increase of the total cross sectional area of palisade cells (fig. 13, A, B, C). Since the epidermal cells expand much more than the attached palisade, a strain obviously results which tends to separate the palisade cells. While the epidermis of the islet has increased about twenty times in area, the adjacent palisade cells in their mid-plane have enlarged meanwhile only eight fold in total cell area. The upper ends of the elongating palisade cells usually expand with the contiguous epidermal cells but small spaces occur even in the junction plane (fig. 9). Lower down these palisade cells separate quite fully and the columnar cells are usually nearly surrounded laterally by air space. It seems clear that the disparity in expansion of epidermis and palisade must set up stresses favoring such separation of interior cells. In *Catalpa* also there is an unequal expansion of

superficial and interior tissues. The epidermal cells increase from $7.9\ \mu$ to $25.8\ \mu$ in diameter, or over nine times in area. At the end of the expansion phase there are four palisade cells to one epidermal cell, each averaging $10\ \mu$ at their mid-plane, a seven fold increase in total cross sectional area of palisade cells in this plane. The fact that the *Catalpa* leaf is more compact is probably correlated with the lesser difference in total expansion of these contiguous layers of the blade.

This greater epidermal expansion seems also to pull apart the spongy mesophyll cells. Their mature form is such as to make accurate measurement difficult but they appear to increase comparatively little in diameter after mitosis ceases which is earlier than in the palisade. The lateral strain placed upon the cells is evidenced by their elongated, lobed outline. This also suggests an explanation of the fact that their longer axes in these species are parallel to the epidermal layers.

Insufficient stress has heretofore been placed upon the mechanico-dynamic function of the epidermis. These layers as noted above appear to be a major factor in leaf expansion, for the veins, while they keep pace with the enlargement of the leaf, are probably not a force in its expansion. Mechanically the epidermis constitutes the only continuous compact tissue between veins and in considerable measure carries and supports the interior mesophyll of the islet.

Time necessary for the development of a leaf

The time required for the development of a foliage leaf is of considerable interest and importance. This study enables one to approximate the length of each epoch in the growth of a *Vitis* leaf. The period from primordium to about 1 cm. in length varies considerably because of seasonal conditions but in midsummer it would probably be passed through in ten days or even less time. The duration of this period of development, however, is relatively unimportant since the leaf is protected meanwhile by overlapping leaves and stipules. By the time the leaf is 1 cm. long it is partly out of the bud and directly affected by external conditions. The time required for a leaf of *Vitis vulpina* to grow from 1 cm. to 12 cm., the length of an average mature leaf, may be estimated with definiteness. Accepting 0.17 cm., given above, as the average rate of growth in length for a leaf under 3 cm. long it will require 11-12

days for the leaf to attain such size. The average daily increase in length obtained for summer leaves over 3 cm. long was 0.5 cm. per day. At this rate it will require an additional 18 days for the leaf to grow from 3 cm. to maturity, or probably 40 days from primordium to adult leaf. No doubt the growth period would be longer under less favorable conditions of earlier spring.

The developmental period is long enough to avoid adjustment to any temporary factors. If this were much reduced accidental shading of part of the leaf for a short time might result in unequal growth of the parts of the leaf. With too short a growth period we might expect the leaf as a whole to be unduly influenced by a succession of sunny or cloudy days while it was expanding. The time, however, is long enough to allow for considerable variations in light and temperature as well as moisture conditions with adjustment to the average environment.

Possibly of great significance is the fact that the growth period of foliage leaves seems ample to permit safe adjustment to the increasing shade within and between branch systems. When leaves emerge from the bud the light is many times brighter for all interior leaves than at the conclusion of their development. There must therefore be a gradual adjustment throughout their plastic phase to average conditions that are to surround the adult leaf during its functional period.

Summary

1. The leaf of *Vitis* or *Catalpa* arises as a lateral protuberance on the stem.

2. The stipules of *Vitis* appear as small protuberances on the central papilla when it is very small (60-100 μ long). *Catalpa* has no stipules and shows no rudiments of them at any stage.

3. Distinct cell layers are evident in the developing leaf. *Vitis* has six of these layers, three of them giving rise to the spongy mesophyll. *Catalpa* may have either five or six, the sixth layer when present becoming part of the mesophyll tissue.

4. *Vitis* shows a more marked apical tip in the embryonic stage and has lateral papillae which develop the lobes and teeth. *Catalpa* which has a smooth margin shows no suggestion of lobing in the embryonic stage.

5. The cell layers begin to differentiate into epidermis, palisade and spongy mesophyll when the blade is 5-8 mm. long.

6. In *Vitis* cell division in epidermal and mesophyll (except cells concerned with vascular development) ceases when the leaf is approximately 2 cm. long. Mitoses continue somewhat longer in the palisade.

7. In *Catalpa* cell division continues until the blade is 15-60 mm. in length. Division continues longer in the palisade cells than in the epidermal. It may also continue longer in mesophyll cells concerned with vascular development.

8. Stomata in both leaves do not all become functional at the same time. Some guard cells are barely differentiated when other stomata of the same leaf region are mature.

9. Growth in both species is uniformly distributed over the leaf blade during the major phases of expansion except that the apical point develops early and soon ceases growth.

10. The development of a *Vitis* leaf under summer conditions from primordium to maturity probably covers a period of 40 days.

11. The upper epidermis of *Vitis* increases in area to more than twice that of the total cross sectional area of the adjacent palisade cells at their mid-plane. The upper epidermis of *Catalpa* also increases in area much more than the total cross sectional area of the contained palisade cells at their mid-plane.

12. The intercellular spaces are schizogenous in origin. The greater expansion of the epidermal layers doubtless tends to separate cells of both palisade and mesophyll tissue and is an important factor in the development of the intercellular spaces.

13. The epidermis not only aids in leaf expansion but provides the major mechanical support of the islet area.

The writer takes pleasure in expressing her thanks to Dr. Robert B. Wylie, at whose suggestion and under whose direction the investigation was carried on, for his helpful advice and criticism.

Ballard Normal School

Macon, Georgia

Plate I *Vitis vulpina*

- Figure 1. Longitudinal section through a bud.
- Figure 2. Outline of a leaf 2 mm. long.
- Figure 3. Transverse section of a leaf 3 mm. long, showing the six meristematic layers.
- Figure 4. Horizontal section of palisade of a leaf about 6mm. long.
- Figure 5. Transverse section of a leaf 10 mm. long.
- Figure 6. Successive stages in the expansion of a single leaf. First three outlines beginning with smallest taken at 24 hour intervals; next three at 48 hour intervals; and last outline after an interval of 72 hours.
- Figure 7. Lower epidermis, surface view, of an immature leaf.

PLATE I

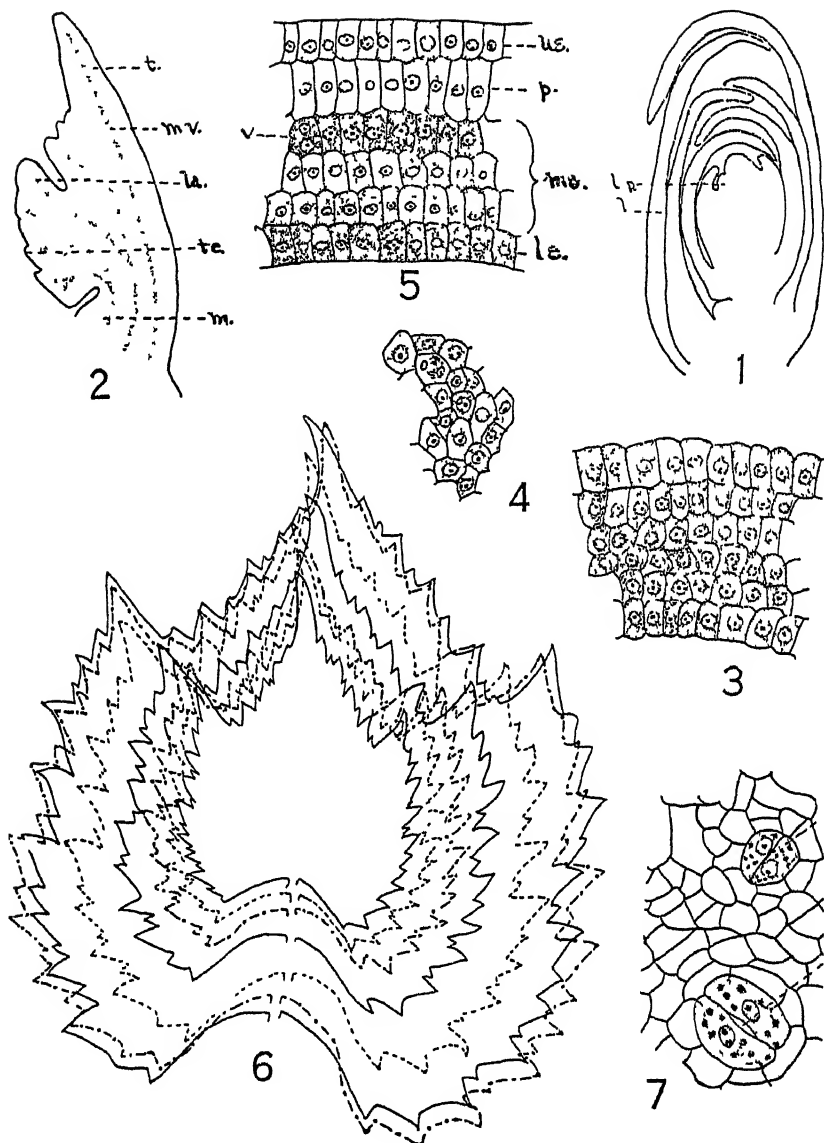


Plate II *Vitis vulpina*

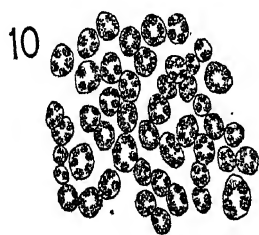
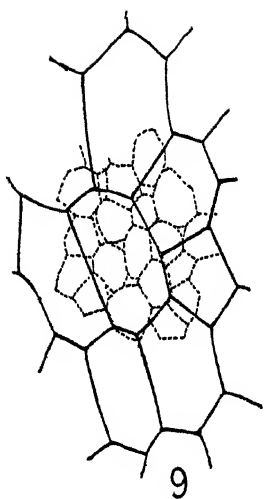
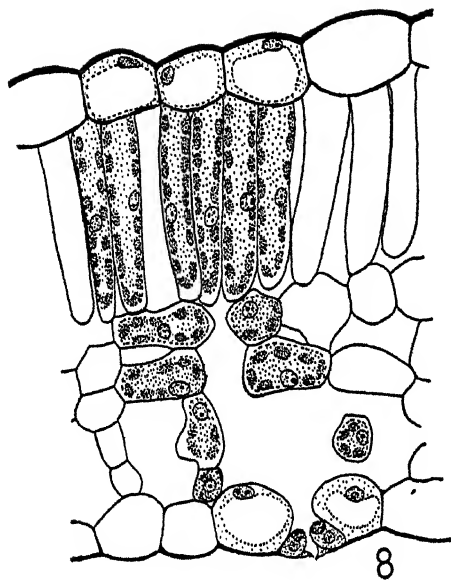
- Figure 8. Transverse section of a mature leaf.
- Figure 9. Upper epidermis, surface view, of a mature leaf. Ends of sub-jacent palisade cells dotted in outline.
- Figure 10. Horizontal section of palisade of a mature leaf, middle plane.
- Figure 11. Horizontal section of spongy mesophyll of same leaf as fig. 10.
- Figure 12. Transverse section of an immature leaf.
- Figure 13. Diagrams drawn to common scale, illustrating the relative enlargement of upper epidermis and palisade cells of *Vitis*, in the horizontal plane.

A. Represents a given area of leaf, involving epidermis and contiguous solid palisade, at the time mitoses cease in the upper epidermal cells.

B. Represents total area in horizontal section of palisade cells developed from the original area (A). Cells measured midway between upper and lower ends.

C. Represents the area of the epidermal cells, included in area A, at the time cell enlargement ceases in the upper epidermis. The disparity in area of the squares B and C represents the unequal expansion of palisade and epidermis of the original area A, as these contiguous layers mature.

PLATE II



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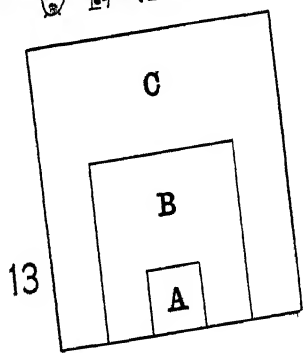
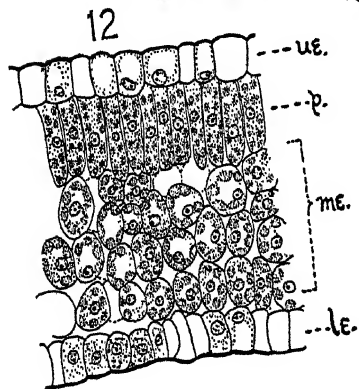
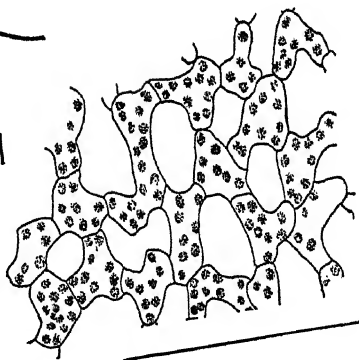
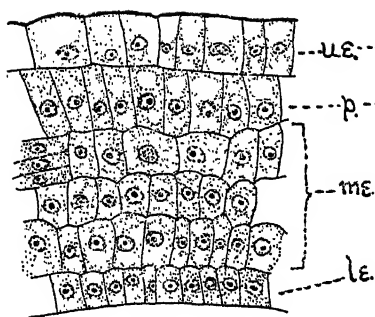


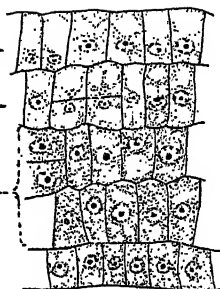
Plate III *Catalpa bignonioides*

- Figure 14. Transverse section of a leaf showing germinal layers.
- Figure 15. Transverse section of a leaf 8 mm. long.
- Figure 16. Transverse section of a leaf 14 mm. long.
- Figure 17. Transverse section of an immature leaf.
- Figure 18. Transverse section of a mature leaf.
- Figure 19. Horizontal section of the palisade of a mature leaf.
- Figure 20. Horizontal section of the spongy mesophyll, same leaf as fig. 19.
- Figure 21. Upper epidermis, surface view, of a mature leaf. Ends of sub-jacent palisade cells dotted in outline.

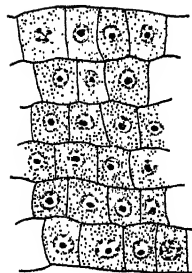
PLATE III



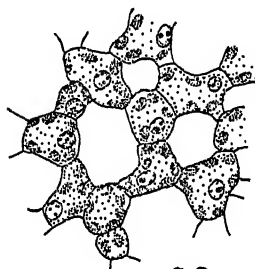
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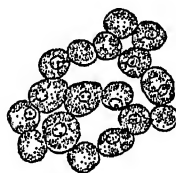
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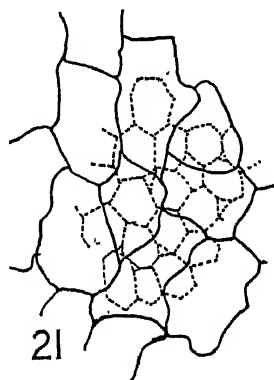
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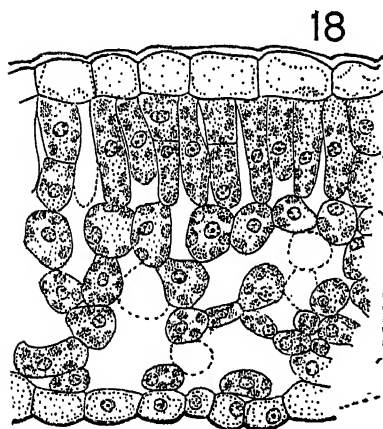
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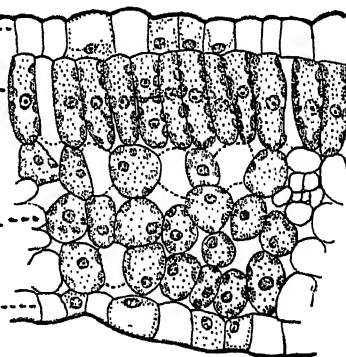


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Development of the Foliaceous Cotyledons of *Cucurbita Maxima*

by

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DEVELOPMENT OF THE FOLIACEOUS (COTYLEDONS OF CUCURBITA MAXIMA

HILMER C. NELSON

In many dicotyledons the seed leaves develop into foliar organs. The shift from storage structure to foliar leaf involves many changes and the morphological transformations in the larger cotyledons may be readily followed. This paper attempts to trace the changes in the cotyledons of the Hubbard Squash (*Cucurbita maxima*) through the germination period.

Cotyledons, in general, may be defined as the first leaves of the plant which do not arise from the primordial meristem. In spermatophytes as summarized by Goebel (5), the cotyledon may serve various purposes, namely (1) as a protective structure investing the bud, such as is found in *Carex*; (2) as a reservoir of reserve material, common in dicotyledons; (3) as a haustorium for the absorption of food for the embryo, common among grains; and (4) as a piston-like structure to push the seedling deeper into the soil during germination, such as is found in *Phoenix*. The above functions are in addition to that of photosynthesis which occurs in certain plants during the later stages of germination.

METHODS

For the anatomical study of cotyledons at various stages during their development sections of living and preserved material were used. Free hand sections were made of various portions of the cotyledon for general study. With the freezing microtome sections were cut parallel and at right angles to the surface. Permanent sections were prepared by the paraffin method in the usual manner. These were cut 10-15 μ in thickness and in the two directions noted above.

Of the various stains used the more satisfactory were an aqueous solution of malachite green and safranin with Delafield's haematoxylin. The former was used to stain temporary mounts prepared by the freezing method, the latter for permanent slides.

To determine the intervacular interval of the mature seed leaves as well as at earlier stages of development, an average of ten

measurements was computed for each of five cotyledons and a final average of these was taken.

To obtain the rate of growth two sets of seedlings were marked and their cotyledons were measured; changes in the dimensions of one set were noted daily and of the other at three day intervals. Measurements of twenty cotyledons (ten plants) were taken at each reading.

In determining the various kinds of stored food present within the cotyledons in the resting seed Eckerson's microchemical tests for aleurone grains, starch and fats were used. The presence of starch was demonstrated by digestion with diastase and by microscopical examination of the cell contents.

HISTORICAL REVIEW

A number of investigators have studied the anatomy of the seed leaf and the changes occurring in embryonic tissues during germination. Hugo de Vries (10) working on clover investigated the external and internal anatomy of the seed as well as the modifications which take place in the different organs during germination. The changes occurring in the constitution of the embryonic tissues and perisperm during germination were followed by Gris (6), who also examined the modifications of the materials which these tissues enclose.

Godfrin (4) studied both tubercular (thick) and foliaceous (thin) cotyledons, making a morphological comparison of their anatomy, as well as the reserve food content of several plants including *Coultaria tinctoria*, *Ricinus*, *Acer* and others. He observed the following relations between the form of the cotyledon and the contents of its cells: (1) foliaceous cotyledons contain only aleurone; (2) tubercular cotyledons contain most frequently a mixture of starch and aleurone grains.

Pée-Laby (7) compared the seed leaves and true foliage leaves on the same plant in reference to their anatomical structure and found a marked similarity between them.

Auenmüller (1) investigated the structure of the cotyledons in the resting seed and the initial changes occurring in the germination of a number of pharmaceutically important plants. In his study of *Cucurbita Pepo* he found the cotyledon to consist of 22-24 cells in thickness and the palisade to be double-rowed, except above the procambial strand where a third row was present. He also

found the seed leaf and radicle to be covered with a delicate cuticle in the resting seed.

In a developmental study of the true foliage leaves of *Vitis* and *Catalpa* Taylor (9) states that in these the intercellular spaces originate through the splitting apart of the cells because of unequal growth. The epidermal cells increased in size more than the contiguous palisade and spongy mesophyll cells and this inequality of growth separates the cells of the layers that expand less along the middle lamellae.

Duggar (3) found in experimenting with Canada field peas that the removal of the cotyledons after the second day of growth depresses the growth rate of the young plant. However, if the seed leaves are removed after seven days, the effect produced upon the rate of growth is very slight when the growth rate is compared with that of the control with cotyledons intact.

After an investigation of the nitrogen metabolism of Hubbard Squash seedlings, Reed (8) concluded that nitrogen compounds are necessary for the maintenance of the leaf, especially if it is exposed to intense illumination for long periods.

GROWTH CHANGES

The beginning of germination is manifested externally by the splitting of the seed coat at the micropylar end. The extrusion of the radicle occurs under favorable conditions after a two or three day period in the soil. This may vary with the rate of oxygen and moisture absorption by the seed coats.

After the radicle appears, growth is quite rapid. The peg grasps a portion of the seed coat by growing around it. The investments are further split apart along the edges, and as the hypocotyl arches up, the cotyledons are soon withdrawn from the seed coats.

Development of the root system keeps pace with that of the hypocotyl and cotyledons. The radicle elongates rapidly, and may achieve a length of approximately nine centimeters by the end of the fifth day. Lateral roots develop as the cotyledons are being withdrawn from the seed coats. Roots with the accompanying root hairs form an efficient anchoring and absorbing system early in seedling life.

EXPERIMENTAL

A number of experiments were carried out to determine the effects produced when parts of the young plants were removed.

EXPERIMENT 1

Marked seedlings grown in sand and supplied with a nutrient solution were divided into three groups. In one division (1) the seedlings were deprived of the plumule, in another (2) one cotyledon was removed and the third group (3) was allowed to develop undisturbed as a control. Measurements of the dimensions of the cotyledons were recorded at three day intervals.

Cotyledons of seedlings in which the plumules were removed experienced a longer period of growth and greater enlargement than the seed leaves in the other groups. It was interesting to note that in the second division the remaining cotyledon on each seedling attained a greater degree of enlargement than either of the seed leaves in the third group. Furthermore the early rate of growth was most rapid in the seed leaves of group 2.

EXPERIMENT 2

Another series of similar experiments was performed with seedlings grown in black soil and supplied with a nutrient solution. In these the plumules were removed from one group (1), the plumule and one cotyledon from each plant in another (2) and

GROWTH RATES OF COTYLEDONS*

October 22 to November 27, 1927

Table 1

Growth Rate in Cotyledons with Plumule Removed

Days after wounding		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	3
Am't of growth over initial measurement	L	9	17	28	37	44	52	57	60	65	68	71	72	74	76	78	8
	W	6	9	15	19	23	27	29	30	32	32	33	34	35	35	35	3
Increments	L	9	8	11	9	7	8	5	3	5	3	3	1	2	2	2	
	W	6	3	6	4	4	4	2	1	2	0	1	1	0	0	0	

Table 2

Growth Rate in Cotyledons after the Removal of Plumule and One Cotyledon

Days after wounding		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	3
Am't of growth over initial measurement	L	13	21	34	44	51	60	64	69	73	76	78	80	81	83	83	3
	W	7	11	19	24	27	31	34	35	36	38	38	39	39	39	39	4
Increments	L	13	8	13	10	7	9	4	5	4	3	2	2	1	2	0	
	W	7	4	8	5	3	4	3	1	1	2	0	1	0	0	0	

* Each record represents an average for ten plants with the exception of the final column which is the average for five plants. L = length in mm. W = width in mm.

Table 3
Growth Rate in Cotyledons of Normal Seedlings

Days		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	36
Am't of growth over initial measurement	L	12	18	22	25	27	30	30	32	33	35	35	35	35	36	36	36
	W	6	10	11	12	12	13	13	13	14	14	14	14	14	14	14	14
Increments	L	12	6	4	3	2	3	0	2	1	2	0	0	0	1	0	0
	W	6	4	1	1	0	1	0	0	1	0	0	0	0	0	0	0

their growth compared with a third group (3) of normal seedlings. Measurements of the dimensions were recorded daily and are shown in tables 1, 2 and 3.

The mutilated plants of the first and second groups developed their cotyledons to two to three times the dimensions of those on normal seedlings. It is of interest to note in this experiment that the cotyledonal growth curves of plants from which the plumules had been removed continue to rise, whereas that of the control seedlings soon straightens out, there being no further enlargement (text fig. 1). This interesting fact is confirmed by the data obtained in experiment 1.

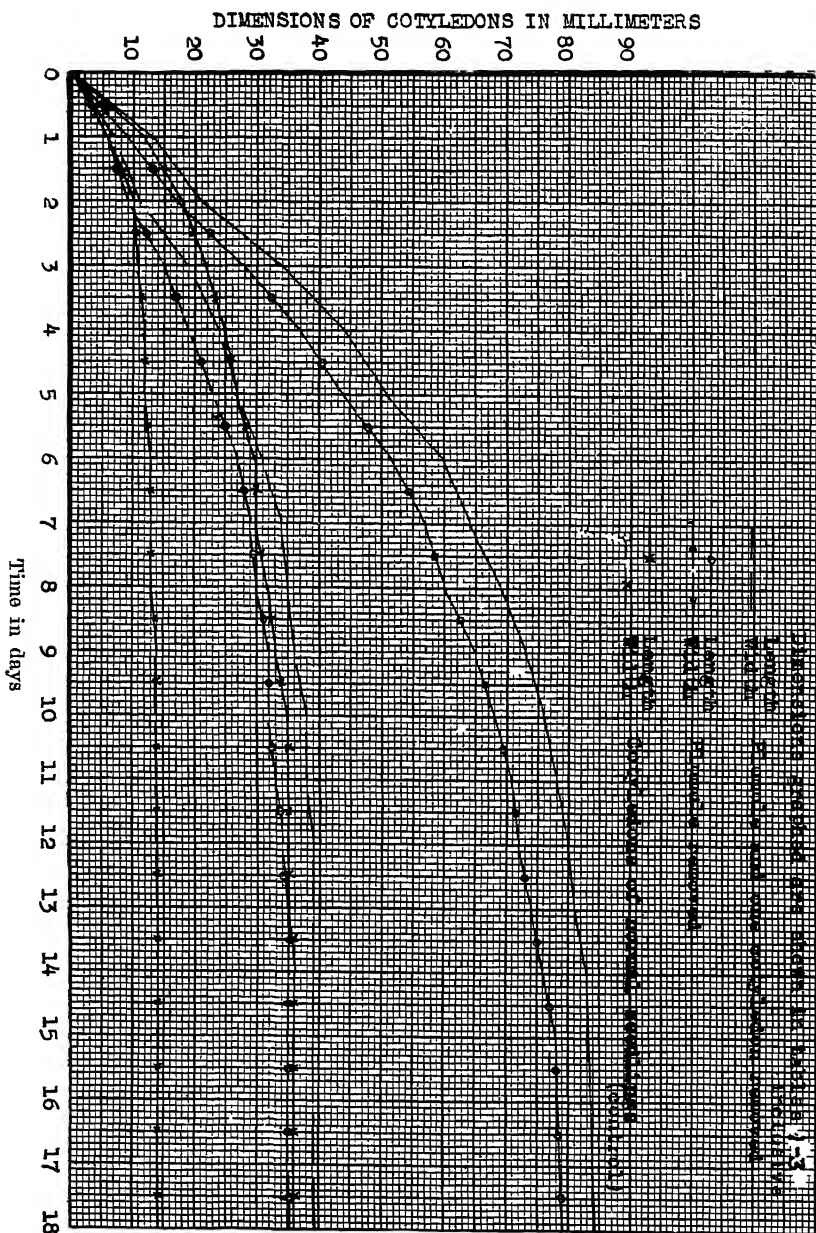
EXPERIMENT 3

In order to determine the effect of cotyledon removal upon the plumule, both seed leaves were removed five days after sowing and at intervals of five days thereafter from successive sets of ten seedlings through a period of twenty days. At the end of the experiment a comparison of the surviving seedlings with normal seedlings was made as shown in figure 1.

A very striking degree of retardation in growth was noted in the initial set in which both cotyledons of each plant were removed at the end of the fifth day; a diminished retardation resulted in the remaining sets of seedlings until the removal of the seed leaves at the end of twenty days produced no visible effect upon the growth of the shoot. Of the seedlings whose cotyledons were removed at the end of the fifth day fifty percent perished.

DISCUSSION

The abnormal enlargement of the cotyledons following plumule removal indicates that the growth inducing agents which normally are translocated to the plumule remain within the cotyledons and stimulate the latter to greater development. Since normal develop-



TEXT FIG. 1. Growth curves of injured and uninjured seed leaves beginning on the fifth day of germination.

ment soon launches large foliage leaves, there is doubtless a correlation between plumule development and the limited size of cotyledons; in other words plumule development hinders cotyledon expansion.

In the light of Reid's experiments (8) it seems altogether probable that more nitrogen was made available to the cotyledons in the form of nitrogen compounds following the removal of the plumule and therefore a greater period of growth was experienced by the former.

The degree of retardation in seedlings deprived of their cotyledons is inversely related to the amount of photosynthetic tissue which was present when the mutilation occurred, for the plants exhibiting the greatest retardation possessed the smallest amount of photosynthetic tissue. The high rate of mortality in these seedlings was caused by a lack of adequate chlorophyll bearing tissue.

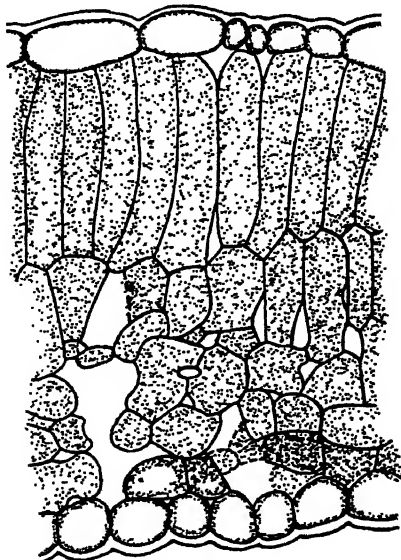
Retardation is due to the removal of food and other growth inducing agents stored within the cotyledon, for the earlier the cotyledons were removed, the smaller was the amount of photosynthetic and non-photosynthetic tissue which was produced by the injured seedlings.

MORPHOLOGY OF COTYLEDONS WITHIN THE RESTING SEED

An examination of the cotyledons of the resting seed revealed the presence of the same general regions as are found in the fully developed seed leaves and in the ordinary foliage leaves as well (text fig. 2, Pl. II, fig. 4 and Pl. III, fig. 9), but the regions are less distinctly differentiated within the resting seed than in the transformed cotyledon. The cell layers in the former are arranged in the following order: upper epidermis 1; palisade 2-3; spongy mesophyll 20; lower epidermis 1. The data refer to the number of cell layers in the central part of the seed leaf. The thickness decreases somewhat toward the edges of the cotyledon. The upper surface of the seed leaf is usually slightly concave and the lower surface is convex.

As indicated above the palisade region consists of two to three layers of cells (Pl. II, fig. 4) which are reduced at the edges to two cell layers. These cells are narrower than those of the spongy mesophyll and have their largest dimension at right angles to the upper epidermis.

The two regions, palisade and spongy mesophyll, merge imper-



TEXT FIG. 2. Transverse section of the ordinary foliage leaf.

ceptibly into each other. In the later stages of development the line of demarcation becomes more distinct due to differences in the shape of the cells and to the compactness of the palisade as contrasted with the large air spaces found in the spongy mesophyll.

The cells of the spongy mesophyll region are initially arranged in more or less vertical rows at right angles to the epidermis, instead of the horizontal arrangement prevalent in the matured photosynthetic seed leaf in which the cells lie more or less parallel with the epidermal cells (Pl. III, fig. 9). In general, the cells of this region are larger than those of the palisade region.

There are present, even before germination begins, small air spaces forming angled openings of varying size at the corners of the mesophyll cells. These are significant in suggesting the method of further development of the air spaces which later become very prominent in the seed leaf.

The upper epidermal cells differ markedly from the lower in size and structure. The former are smaller than the latter and have thinner cell walls. There are no stomata present in either upper or lower epidermis of the cotyledon in the resting seed. An extremely thin cuticle extends over the outer walls of all epidermal cells. The principal procambial strands are usually nine in number, and there are no traces of lignification at this stage.

RESERVE FOODS OF RESTING SEEDS

The reserve food material in the resting seed was found to consist of aleurone, fat and starch. The aleurone grains are the most abundant food material within the cells at this stage, as reported by Barber (2) for *Cucurbita Pepo*, and are found in all cells of the cotyledon of the squash. Fats also form a large part of the food reserves and seem to be concentrated to a large extent in the epidermal cells. Starch is present apparently only in small quantities, for direct tests fail to reveal its presence. Nevertheless, the grains were visible in cells when they were highly magnified, and digestion with diastase gave evidence in support of this observation.

The food materials disappear first from the epidermal and procambial cells and last from the spongy mesophyll. Practically all of the reserves have been digested by the end of the fifth day following planting. At this stage the cotyledons are either emerging from the soil or have already assumed a horizontal position above the ground (Pl. I, figs. 2, 3). In either case photosynthesis

has begun and as the photosynthetic activity increases, there is built up a reserve of starch in the seed leaves.

DEVELOPMENT AND DIFFERENTIATION OF CELL REGIONS

Stomata are present on the third day following planting. Their development is the same as that in the true foliage leaves and as the guard cells enlarge, an intercellular space forms beneath them.

The cuticle of the seed leaf remains quite thin until the tenth day of germination when local thickenings were observed bordering the guard cells at the stomatal openings. The presence of the cuticle was demonstrated by means of Sudan III (.5 gms. in 100 cc. of 70 per cent alcohol).

Trichomes make their appearance on the dorsal surface of the cotyledon during the second day after planting. At this stage the hairs may be protrusions consisting of one to three cells. These usually divide transversely resulting in the production of multicellular glandular or non glandular hairs. The former are stalked globular structures, whereas the latter are usually broad at the base and taper abruptly to slender pointed tips.

The lower epidermis shows the beginning of trichome development on the second day following that in the upper surface. At this time they are composed of only one or two cells. It may be significant to note that at this stage the cotyledons are being withdrawn from the seed coats (Pl. I, fig. 2), and that as long as the lower epidermis is in contact with the seed coat no development of epidermal hairs takes place. All trichomes are similar in their morphology and they occur most abundantly on the upper epidermis.

Changes in the size and form of the epidermal cells are marked and of considerable importance. These cells, examined twenty-four hours after planting, were apparently of the same size as those in the resting seed, but by the second day they averaged much smaller due to divisions in the peripheral cell layers. Cell multiplication proceeds so rapidly in the upper part of the cotyledons while the latter are still within the seed coats during the third and fourth days of growth, that the epidermal and adjacent palisade layers become depressed into furrows which extend into the spongy mesophyll of the seed leaf. No furrows were found in the lower side, although the cells in this region are also dividing.

The dorsal grooves disappear during the fifth day as the cotyledons are being withdrawn from the seed coats.

The enlargement phase begins in the upper epidermis during the fifth and sixth days. It is evident at this time that some of the cells in this layer are undergoing division, whereas, others are enlarging.

All cell layers of the cotyledon have entered the enlargement phase by the seventh day of development. The lower epidermal cells are now slightly larger than those of the upper peripheral layer, and it is at this time that the wavy lateral walls characteristic of lower epidermal cells appear.

A steady increase in the size of cells of the peripheral layers continues from the seventh to the twentieth days of germination, with the cells of the lower epidermis continuing somewhat larger than those of the upper layer. Examination of sections at the thirty day stage showed no further enlargement in these layers over the twenty day stage.

The first day's growth reveals little change in the palisade of the cotyledon. Sections of cotyledons which have remained for two days in the soil show that the cells in this region are noticeably narrower than those in the corresponding part of the resting seed and have apparently begun cell division which continues through the third, fourth and fifth days of growth (Pl. II, figs. 5, 6). Cell enlargement begins in the palisade during the seventh day of development and continues for two weeks (Pl. III, figs. 7, 8).

The most conspicuous changes in the development of the seed leaves are in the region of the spongy mesophyll. These cells apparently remain undivided throughout the transformation of the cotyledon into the foliar organ despite the active cell division and enlargement occurring in the other regions of the seed leaf. Extensive changes occur, however, not only in the amount of air space in this region, but also in the volume and form of the cells.

Transverse and horizontal (cut parallel to the epidermis) sections of the dormant cotyledon show small angular spaces at the corners of the cells in the palisade and spongy mesophyll regions. Sections of cotyledons one day after planting show no variations, but one day later a slight increase was noted in the degree of air space development at the corners of the cells. This change continues during the third and fourth days of growth and by the end

of the fifth day an extensive system of air spaces is present (Pl. IV, fig. 10).

By the seventh day many of the mesophyll cells have undergone a change in relative position so that some are elongated parallel with the epidermis, while others still remain at right angles to the peripheral layers. The volume of these cells has become considerably enlarged, and many show a distinct lobing at the corners.

In the final arrangement most of the spongy mesophyll cells have either become spherical or have elongated in the dimension parallel with the peripheral layers (Pl. III, fig. 9). While the epidermal and palisade cells have undergone a period of division followed by enlargement, the spongy mesophyll cells have enlargement without mitoses. Air spaces have become much more extensive in the spongy mesophyll than in the palisade region. Apparently the epidermal cells have increased in size and number more rapidly than the mesophyll cells, and this inequality of growth has pulled apart the cells which enlarged less. This development is similar to that of the true foliage leaves of *Vitis* and *Catalpa* as reported by Taylor (9).

The same spreading venation is found in the seed leaf as occurs in the true leaf with this difference: that the veins of the cotyledons do not unite at the base, but extend separately into the petiole and stem. There are seven major veins in the cotyledon which vary considerably in length and degree of development. From these numerous lateral veins branch forming a reticulate network in the lamina of the seed leaf.

The vascular regions (procambial strands) in the resting seeds are filled with stored food. The cell walls are quite thin with no traces of thickenings present in the walls of the cells destined to become the vessels. Increase in thickness of walls begins promptly, for in seeds that had been soaked in water for seventeen hours and placed in the soil for twenty-four hours, a few less dense cells in the procambial strand were found with thickened walls. Seed leaves one day later showed a few well developed vessels in the principal vascular strands. The central strands also contained a large number of cells emptied of their food reserve. Vascular bundles three days after planting revealed the presence of more than a dozen thick-walled vessels; the remaining cells in the bundle, emptied of their food reserve, were undergoing differentiation into their respective tissues.

The cotyledon possesses an efficient minor venation. There are two systems of these veins (1) those that ramify through the lower part of the spongy mesophyll, which are well developed and supported by mechanical cells and (2) those that spread through the upper part of this region directly beneath the palisade layer, which are very simple and more abundant. The intervascular interval between these palisade veinlets becomes greater as the seed leaf increases in size, but is less in the mature cotyledon than in the foliage leaf.

The intervascular intervals of palisade veinlets (second system of minor veins) of cotyledons and foliage leaf measured from the edge of one veinlet to that of the other are as follows: cotyledon of dormant seed .064 mm.; seed leaf after five days growth .084 mm.; average of mature cotyledons aged 40, 43, 37, 82 and 40 days .136 mm.; foliage leaf .146 mm. Each of the preceding records represents an average of fifty measurements in five cotyledons, and the same number in the foliage leaf.

DISCUSSION

The palisade, spongy mesophyll, and epidermal tissues of the cotyledons are first specialized for food storage and are not distinctly differentiated within the resting seed. During germination changes in the morphology of these cells accompany changes in function enabling the transformed seed leaves to perform efficiently the work of a foliage leaf. The large quantity of protein stored in the cells of the resting seed makes possible the rapid development of the seedling. The evidence indicates that the small angular spaces at the corners of the mesophyll cells within the cotyledons of the resting seeds are formed by the separation of the cell walls along their middle lamellae. The subsequent enlargement of these intercellular spaces produces the extensive system of air spaces adjoining the mesophyll cells of the transformed cotyledon.

The temporary furrowing of the upper surface of the cotyledon is probably caused by a greater proliferation of cells in the upper epidermis and palisade region than in the mesophyll and lower epidermal layers. Unable to expand laterally due to the constricting effect of the seed coats, these tissues were forced downward compressing the spongy mesophyll which at this time was being rapidly exhausted of its food reserve. It seems probable that the force exerted by the dividing and enlarging cells of the peripheral

layers directed against the edges of the seed coats caused a further extension of the splitting already begun at the point where the radicle and hypocotyl had emerged.

Sections show that coincident with the expansion of the cotyledon in the initial phases of germination, the epidermal and palisade cells undergo repeated division and enlargement as contrasted with a less degree of enlargement in the spongy mesophyll, causing the cells in the latter region to be subjected to lateral tension.

The separation of the spongy mesophyll cells takes place along the middle lamella and results in the production of a large number of air spaces. It seems probable also that since the epidermal cells divide and enlarge more rapidly than the contiguous mesophyll, this unequal growth causes air spaces to develop in the palisade region. These changes resulting in an extensive system of air spaces are essentially like those described by Taylor (9) as occurring in the development of the true foliage leaves of *Vitis* and *Catalpa*.

The intercellular spaces formed during germination are merely enlargements of the small angular spaces at the corners of the cells in the resting seed and seem to have resulted from tensions due to unequal growth of the several cell layers.

Vascular differentiation may begin very early after the planting of the seed, as shown by the launching of vessels in the chief procambial strands of the cotyledon within twenty-four hours. These vessels are undeveloped in the resting seed and therefore their appearance is associated with the beginning of seedling development.

The differentiation of the conducting tissues keeps pace with the increase in the size of the cotyledon. The intervacular interval is less in the developing than in the mature seed leaf, making possible rapid translocation of food reserves during the critical period of germination.

Since the intervacular interval of the seed leaf is less than that of the true leaf, translocation of materials may occur more speedily in the cotyledon than in the true foliage leaf.

SUMMARY AND CONCLUSIONS

1. The cotyledons of *Cucurbita maxima* in the resting seed contain the same general regions as are present in the mature foliar cotyledon.

2. Stomatal development occurs in the same manner as in the ordinary foliage leaf.

3. A thin cuticle is present in the resting seed as a delicate covering over the cotyledons.

4. Trichome differentiation begins early in the process of germination and starts first on the upper epidermis.

5. Germination begins within twenty-four hours after planting and may continue for twenty days, or until the supply of growth inducing substances within the cotyledons is exhausted.

6. Cell division begins as early as the second day of development and continues through the fifth day.

7. Cell division predominates in the epidermal layers and palisade zone of the seed leaf from the second to the fifth day of germination, after which cell enlargement begins and continues until the seed leaf becomes mature.

8. Cells in the epidermal and palisade layers divide and enlarge more actively than in the associated spongy mesophyll region. The lateral expansion of the cotyledon seems to be due primarily to the division and enlargement of epidermal cells.

9. The organization of the spongy mesophyll is doubtless aided by tensions, due to the unequal growth of this zone compared with the adjacent layers.

10. The spongy mesophyll cells seldom divide, enlarge early, become spherical and then elongate laterally parallel to the epidermis. The greatest development of the intercellular space occurs in this region.

11. Growth in area is distributed uniformly throughout the seed leaf.

12. There is a definite correlation between plumule development and the size of cotyledons.

13. The presence of normal cotyledons on the seedling during germination is essential for the unimpeded development of the plumule.

14. The cotyledon possesses two general groups of minor veins, one in the palisade and the other in the spongy mesophyll.

15. The intervascular interval between the palisade veinlets becomes greater as the cotyledon increases in size, but is less in the mature foliar cotyledon than that between the veinlets in the true foliage leaf.

16. Normal development of the cotyledon to maturity from the seed condition probably covers a period of about twenty days. This period may be lengthened to approximately thirty days by the removal of the plumule immediately after the appearance of the cotyledons above the soil during germination.

17. The intercellular spaces result from a separation of the walls of the mesophyll cells along the middle lamella.

This report is the result of a two years' study of the morphology of cotyledons under the direction of Professor R. B. Wylie, Head of the Department of Botany of the State University of Iowa, to whom the writer is deeply grateful for helpful advice and criticism and for his suggestion of this problem.

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EXPLANATION OF PLATES

PLATE I

Fig. 1. Photograph of seedlings showing the effects of cotyledon removal upon their development: *a-f* showing retardation caused by the removal of seed leaves five days after planting; *g-i* exhibiting delayed development following the removal of cotyledons ten days after planting; *j, k*, showing retarding effect after the removal of the cotyledons fifteen days following planting; *l, m*, showing no effect after the removal of cotyledons on the twentieth day; *n, o*, normal seedlings with seed leaves intact. Age of all plants is twenty-six days.

Figs. 2-3. Successive stages in the development of squash seedlings.

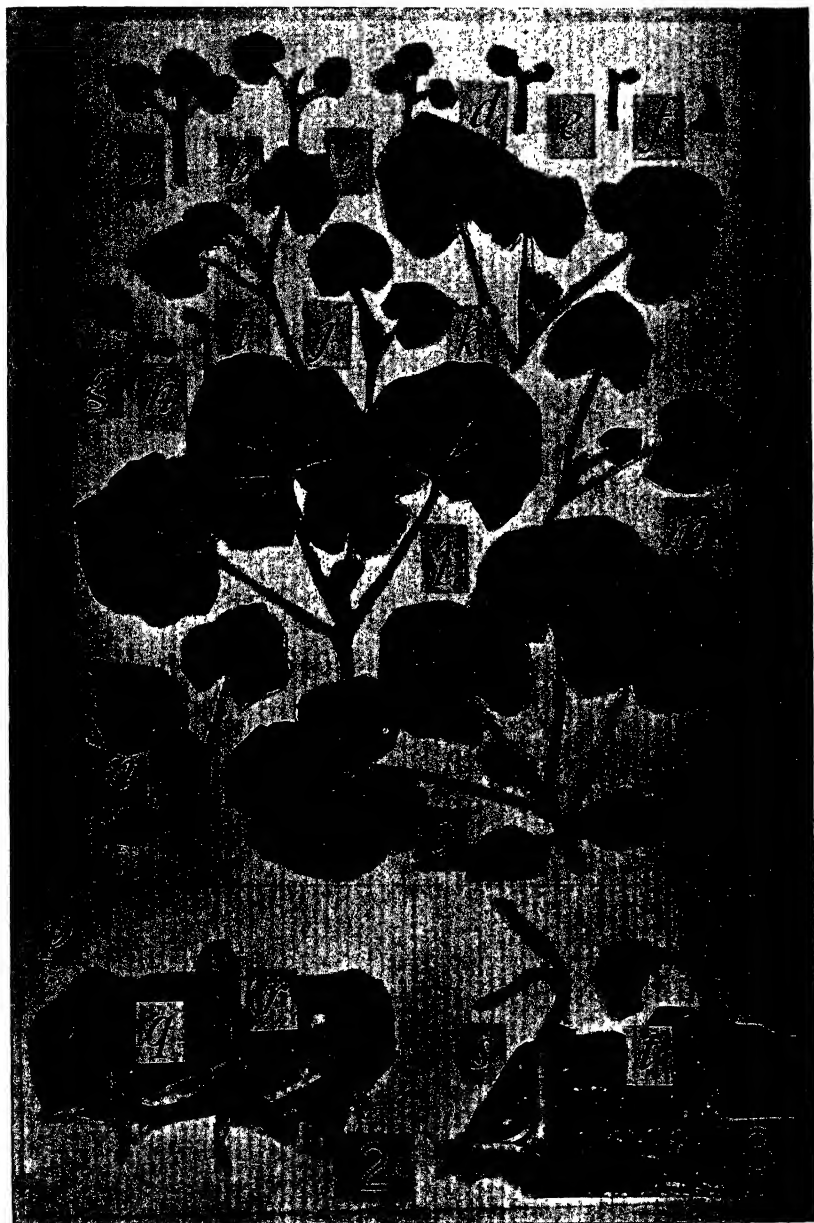


PLATE II

Fig. 4. Transverse section of cotyledon in dormant seed condition. x154.

Fig. 5. Transverse section of cotyledon after a five day period in the soil showing large air spaces in spongy mesophyll. x154.

Fig. 6. Transverse section of seed leaf after soaking in water for twelve hours and one day's sojourn in the soil. x154.

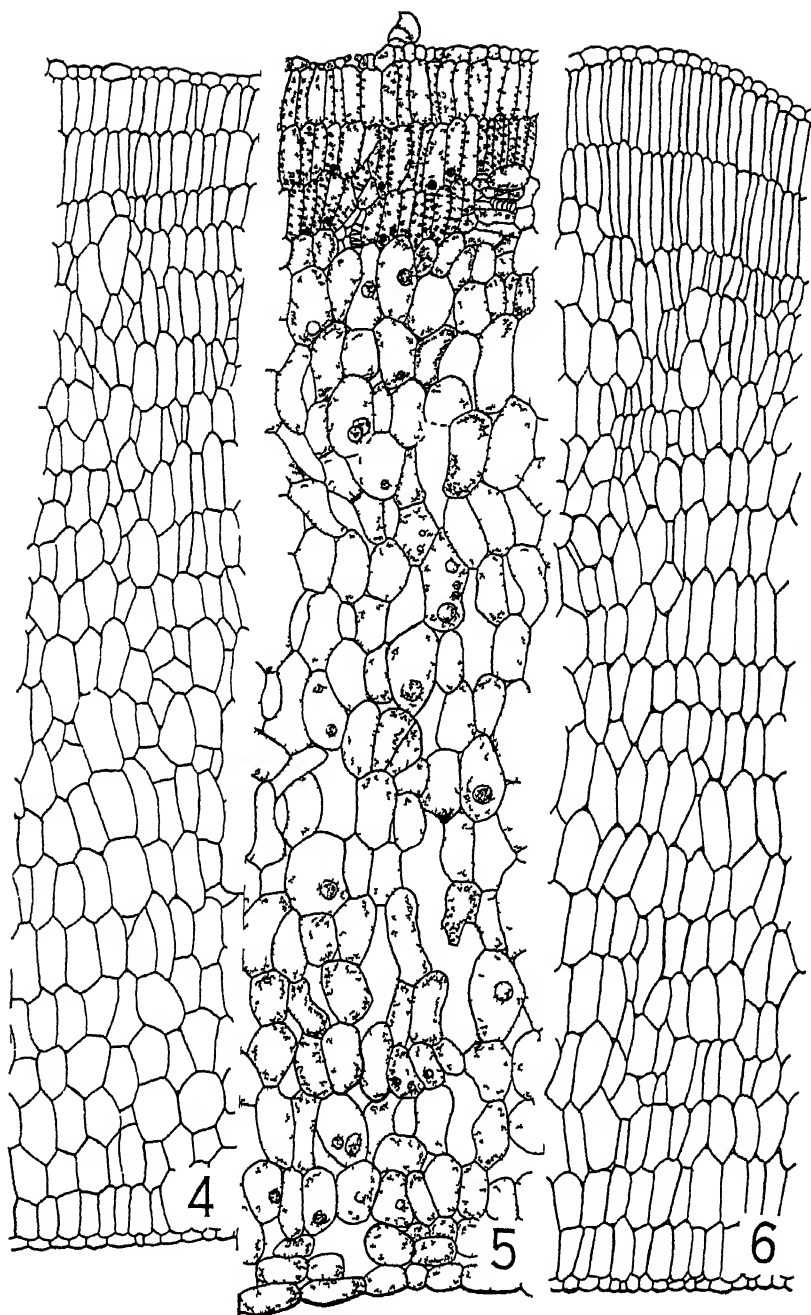


PLATE III

Fig. 7. Transverse section of seed leaf showing extent of development on the seventh day of growth. x154.

Fig. 8. Transverse section of cotyledon fourteen days after planting. x154.

Fig. 9. Transverse section of seed leaf on the thirtieth day showing transformed spongy mesophyll cells. x154.

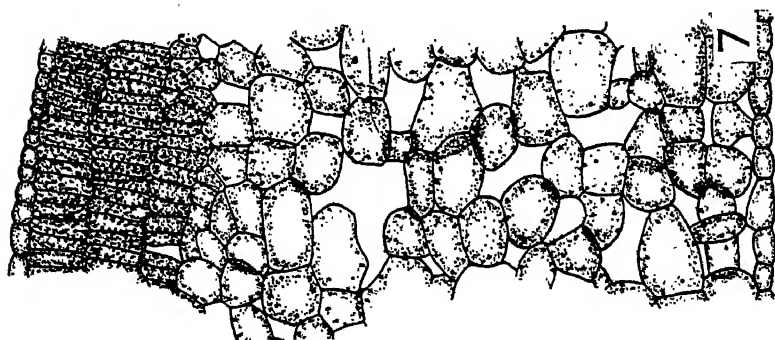
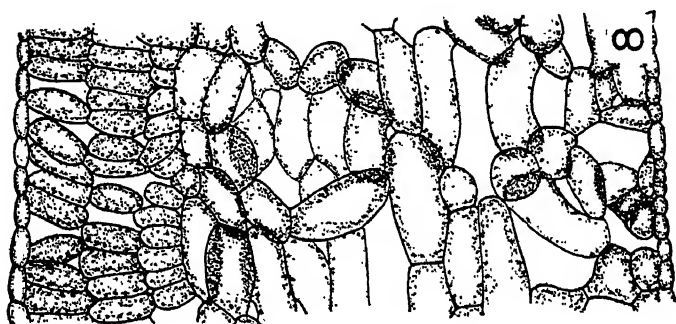
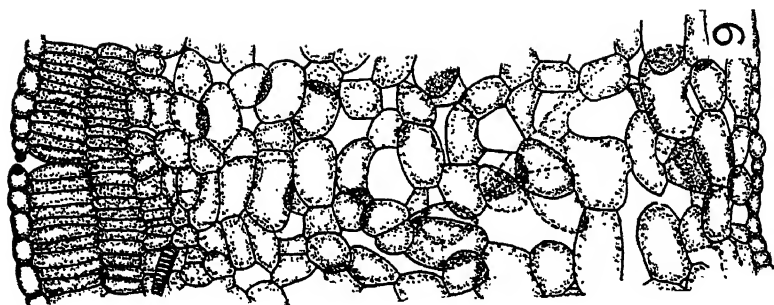
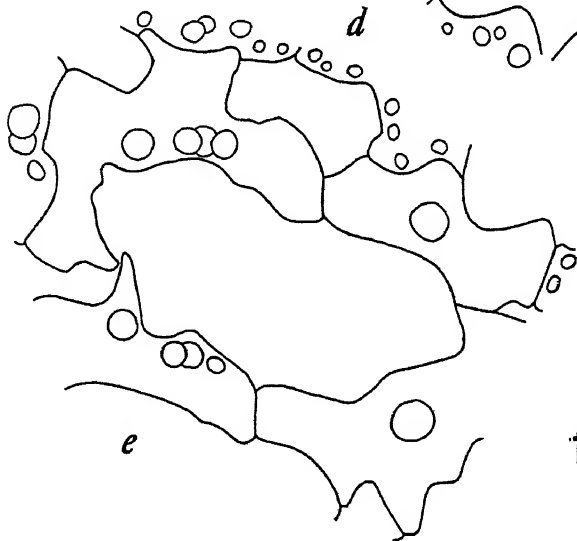
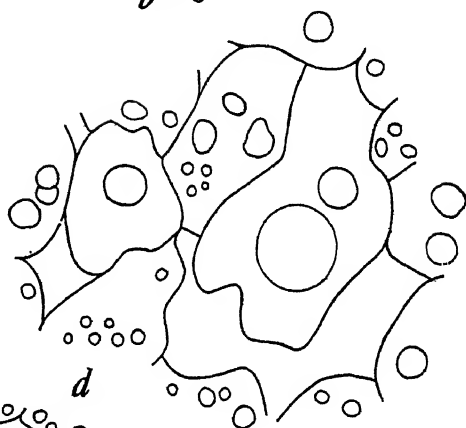
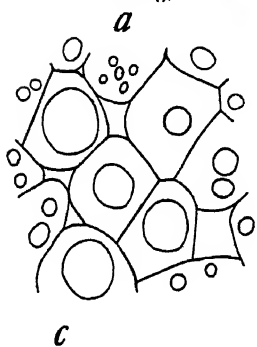
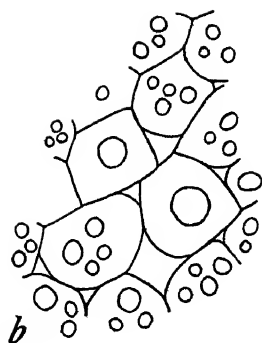
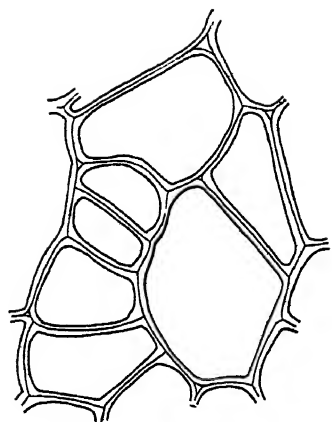


PLATE IV

Fig. 10. Sections cut parallel to the peripheral layers showing structure of seed leaf five days after planting: *a*, showing cell enlargement and stomatal development in upper epidermis; *b*, *c*, showing reserve food within the cells and development of air spaces in upper and middle portions of the palisade region; *d*, *e*, showing reserve food within the cells and development of air spaces in middle and lower portions of the spongy mesophyll.

All drawings were made with the aid of a camera lucida and a Zeiss apochromatic objective 90 n. a. 1.30 and ocular 10x.



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A KEY TO THE MOSSES OF THE OKOBOJI REGION

by

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A KEY TO THE MOSSES OF THE OKOBOJI REGION*

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The Okoboji Region as here understood includes the area readily available to botanists working at the Iowa Lakeside Laboratory, namely Emmet, Dickinson, Osceola and Lyon Counties, Iowa, the Sioux Quartzite outcrops in Brown and Cottonwood Counties, Minn., and the vicinity of Heron Lake, Minn. No additional species have been found in brief forays in Palo Alto, Clay, O'Brien, Sioux, Plymouth, Woodbury, Cherokee, Webster and Kossuth Counties, so that these counties may be considered to be included in the list. It covers, therefore, the known mosses of northwestern Iowa. Additional species appear in Winnebago County, and become more numerous eastward.

The list of species in this key is based upon Wolden's "Moss and Lichen Flora of Western Emmet County" (8), and subsequent collections of Wolden published by Blagg (2, 3, 4). We have recently collected together in most of the region, under guidance of Mr. Wolden, seeing again the majority of the species and adding a few which are here published for the first time for the area. The lists published by Shimek (7) and Cavanagh (5, 6) have also been considered and we entered in the Key those species which through the kindness of Miss Cavanagh, we have seen. Species not seen, and for which therefore we cannot assume responsibility, are given in footnotes.

The identifications of Wolden's Emmet County list were by G. B. Kaiser of the Sullivant Moss Society. Later material has been checked by A. LeRoy Andrews, E. B. Bartram, A. J. Grout, G. R. Jones and G. B. Kaiser, to all of whom we are indebted. *Amblystegium* and *Drepanocladus* were referred to Grout. Specimens of all species given in the key, excepting *Amblystegium brevipes*, *Bryum intermedium* and *Orthotrichum anomalum* are accessible in the herbaria of the authors. Species marked with an asterisk (*) have been collected by Wolden in Emmet County.

* Contribution from the Iowa Lakeside Laboratory.

A number of names found in the published lists are believed to be in error:

Hypnum fluitans is probably our *Drepanocladus aduncus*.

Ephemerum sessile cannot be found or verified.

Fabronia gymnostoma, kindly communicated by Miss Cavanagh, we believe to be better referred to *F. octoblepharis*.

Amblystegiella subtilis, *Bryum inclinatum*, *Campylium radicale*, *Catharinea crispa*, *Drepanocladus vernicosus*, *Fissidens adiantoides*, *F. bryoides* and *F. subbasilaris* are found to be wrongly identified.

Authorities for names are not cited, since the names are understood to be as given in Grout's "Mosses with hand-lens and microscope". *Grimmia poecilostoma* (Card. & Seb.) Limpr., identified by G. R. Jones (*G. glauca* and *G. leucophaea* of other lists) is not given in Grout's book. The species of *Amblystegium* and *Drepanocladus* are treated in harmony with Grout's "Moss Flora of North America." The student will not be satisfied with the meager descriptions afforded by the Key, but will want to have at hand a suitable manual. Hence the reference to Grout, and the retention of his names.

The Key is obviously patterned after Grout, but an attempt has been made to include both leaf and capsule characters, wherever both are diagnostic. Thus both sterile and fertile material can be traced in the same key. Helpful corrections and modifications will be welcomed by the authors.

We are indebted to the Administration of the State University of Iowa, and especially to Professor G. W. Martin, Director of the Iowa Lakeside Laboratory, for the use of the facilities of the Laboratory (which gave us the opportunity to work together) and for the privilege of publishing under their auspices.

KEY TO GENERA

1. Plant thalloid: a green scale-like growth, without distinction of stem and leaf (Fig. 1-3) Hepaticae
1. Plant showing stem and leaves (Fig. 11, 14, 27, 29, 40) 2
2. Lvs. 2-ranked (dorso-laterally), without midrib, the cells isodiametric; sporophyte short-lived (Fig. 11-19) Hepaticae
2. Lvs. with midrib; or if without midrib, many ranked, the leaf or the cells or both elongate; sporophytes persisting for weeks or months (Fig. 21-52) Musci

HEPATICAE

1. Plant thalloid: a green scale-like growth (Fig. 1-3, 20) 2
1. Plant showing stem and leaves (Fig. 11, 14, 19) 11
2. Thallus watery-translucent, without air spaces 3
2. Thallus opaque, with air chambers 4
3. In rosettes to 2 cm. across; capsule erect, rod-like, long lived (Fig. 20) 14. Anthoceros
3. In small (to 2 cm. long) irregularly pinnate-lobed thalli, in water or marshes (Fig. 10) 7. Aneurua
3. In clustered running thalli, each 5-10mm. across; on moist earth 8. Pellia
4. Without visible pores opening into air chambers 5
4. Surface showing polygonal areas, with an air pore in each polygon (Fig. 7) 9
5. On earth 6
5. In water, floating 8
6. On upland soil or rocks; margins red-purple beneath; purple scales with 2 linear appendages (Fig. 9). 6. Reboulia
6. On margins of ponds; without scales; green 7
7. Thalli very numerous, 1-2mm. wide, in dense beds (Fig. 1) 1. Riccia
7. Thalli 1-few in a place, 2-4mm. wide (Fig. 2) 2. Ricciocarpus
8. Thalli 1-2mm. wide, 5-25mm. long, branched (Fig. 1) 1. Riccia
8. Thalli 2-10mm. across, about as long as wide (Fig. 2) 2. Ricciocarpus
9. Polygons 1-1.3mm. across; pore at tip of a colorless mound (Fig. 5) 3. Conocephalum
9. Polygons 0.5mm. across or smaller; pores barrel-shaped 10
10. With marginal scales beneath; gemmae cups common (Fig. 3, 4) 4. Marchantia
10. No marginal scales or gemmae; rare (Fig. 6) 5. Preissia
11. Lvs. with an underlobe, incubous; underleaves present (Fig. 11, 12) 12
11. Lvs. without underlobes, succubous (Fig. 14, 19) 13
12. Underlobe forming a helmet-shaped sac; shoots ½mm. wide (Fig. 12, 13) 9. Frullania

12. Underlobe not sac-like; shoots 1-2mm. wide (Fig. 11)10. *Porella*
 13. Some or all lvs. notched at apex (Figs. 14, 15, 18)12. *Lophocolea*
 13. Lvs. rounded; no underleaves; shoots 1mm. wide or less (Fig. 19)
13. *Jungermannia*
 13. Lvs. obovate; underleaves minute, wedge-shaped; shoots 2-3 mm. wide
11. *Plagiochila*

MUSCI

1. Lvs. long and narrow, with parallel vertical plates of cells (Fig. 22, 23)
 on upper surface of midrib; teeth of peristome 32 or 64, not transversely
 jointed or barred (Fig. 21)*Nematodontae* Polytrichaceae 2
 1. Lvs. without vertical plates; teeth 8, 16 or 32, transversely jointed or
 barred, or absent (Fig. 26, 30, 36) *Arthrodontae* 3
 2. Lvs. without green lamina (Fig. 22), but with membranous sheathing
 base; caps. stout, angular; calyptra hairy15. *Polytrichum*
 2. Lvs. with distinct lamina, not sheathing at base (Fig. 23); caps. slender
 cylindric; calyptra hairless16. *Catharinaea*
 3. Lvs. 2-ranked, split at base, clasping stem and next leaf above; with mid-
 rib (Fig. 28)17 *Fissidens*
 3. Lvs. not split along upper margin 4
 4. Plants erect, unbranched except for annual renewal of growth; seta from
 tip of stem (or apparently lateral because of renewal shoots) (Fig. 25-29)
Acrocarpi 5
 4. Plants creeping widely, branching continuously, sometimes with erect
 shoots (Fig. 40-52); seta from a lateral bud29

ACROCARPI

5. Lvs. papillose, without midrib; often white-tipped; on rocks; caps. covered
 by lvs., without peristome 22. *Hedwigia*
 5. Lvs. papillose, with midrib (Fig. 24, 35) 6
 5. Lvs. not papillose, or only faintly so on upper back15
 6. Leaf margin rolled upward (involute) (Fig. 31) 7
 6. Leaf margin rolled backward (revolute), at least above 8
 6. Leaf margin plane (not rolled); tiny tufted rock-moss without peristome
 (Fig. 35)25. *Gymnostomum*
 7. Seta distinct, 5-15mm.; peristome imperfect (Fig. 31)24. *Weisia*
 7. Seta shorter than capsule; without operculum23. *Astomum*¹
 8. Lvs. evenly tapering from base to slender apex11
 8. Lvs. ovate or tongue-shaped, with a point or hair on the rounded tip 9
 9. Tip composed of the excurrent midrib; peristome of twisted threads10
 9. Tip made of single cells beyond tip of rib; peristome white, imperfect
 (Fig. 24)27. *Desmatodon*
 10. Leaf tip very short and stout; peristome wholly of threads26. *Barbula*

¹ *Phascum floeridianum*, lvs. revolute, "on open drift hill near West Okoboji Lake" is reported by Cavanagh (6).

10. Leaf tip slender, hair-like; peristome threads from a netted basal membrane (Fig. 26) 28. *Tortula*
11. Lvs. entire 12
11. Lvs. irregularly crenate near apex; capsule elongate, ribbed 35. *Anacamniun*
11. Lvs. distinctly and sharply serrate; caps. nearly globular, with mouth on one side of tip 14
12. On earth or earthy rocks; peristome twisted; seta about 1cm. tall 26. *Barbula*
12. On bark, well above ground (Fig. 27) 30. *Orthotrichum*
12. On rocks, firmly attached, independent of soil 13
13. Peristome teeth erect when dry 30. *Orthotrichum*
13. Peristome teeth folded back against outside of capsule when dry 29. *Ulot*
14. Lvs. very slender, recurved; plants of wooded banks (Fig. 25) 37. *Bartramia*
14. Lvs. ovate-lanceolate, erect or spreading; in very wet places 36. *Philonotis*
15. Very black tufted moss on rocks; caps. covered by lvs.; teeth red 21. *Grimmia*
15. Ordinary green mosses; midrib present 16
16. Lvs. oval; cells small, isodiametric, thick-walled; peristome of twisted threads from a netted basal membrane (Fig. 26) 28. *Tortula*
16. Lvs. oval (1:5 or less); cells large, distinct 17
16. Lvs. long, slender (1:6 or more); pointed 23
17. Cells rectangular, distinct; lvs. clustered at ground level on the very short stems; annuals (Fig. 29) 18
17. Cells hexagonal; lvs. 5-10mm. long, in a rosette at top of a stem 1-2cm. tall; perennial (Fig. 37) 43. *Rhodobryum*
17. Cells hexagonal to rhombic, or rarely elongate; lvs. equally placed along a distinct stem; caps, nodding 20
18. Caps. erect, globular or bowl-shaped, without peristome; lvs. sharply toothed in upper half (Fig. 29) 19
18. Caps. nodding, pear-shaped, the operculum to one side of tip (Fig. 32); lvs. entire or nearly so 33. *Funaria*
19. Caps. immersed (no seta) 31. *Aphanorhegma*
19. Seta distinct; caps. above lvs. (Fig. 29) 32. *Physcomitrium*
20. Caps. barrel-shaped; stems often rooting at tips (Fig. 39) 44. *Mnium*
20. Caps. pear-shaped (Fig. 33); stems strictly erect, usually densely tufted 21
21. Lvs. relatively far apart, the chlorophyll sparse (in flecks on cell walls when dry) 40. *Mniobryum*
21. Lvs. crowded or close, evenly green (or white-tipped) 22
22. In dense sods everywhere; lvs. spreading when moist, or julaceous and white tipped 41. *Bryum*
22. Stems julaceous, flagelliform; cells narrow; very rare, on Sioux quartzite 42. *Anomobryum*
23. Lvs. 5-6mm. long, with stout midrib 24
23. Lvs. less than 5mm. long 26

24. Lvs. suddenly narrowed to tip, toothed near apex; inner peristome entirely of cilia (Fig. 34) 34. *Timmia*
24. Lvs. very finely tapered from base to apex 25
25. Lvs. all curved to one side, channelled; toothed on back of midrib; plants in big cushions 20. *Dicranum*
25. Lvs. hairlike, wavy; caps. pear shaped, nodding 38. *Leptobryum*
26. Tiny tufted annuals with caps. sessile among the lvs.; no peristome see footnote 2.
26. Seta and peristome well developed; perennial 27
27. Margins plane 28
27. Margins revolute nearly to the finely toothed apex; seta and inclined caps. mahogany red (Fig. 38); common 18. *Ceratodon*
27. Lvs. channelled by upturned margins, or plane and entire; caps. erect, or kinked to one side below the mouth; teeth split half way down 19. *Dicranella*
28. Lvs. toothed above; with strong midrib; caps. large, nodding; mesic 39. *Pohlia*
28. Lvs. entire, without midrib; in bogs 57. *Campylium*
29. Lvs. apparently 2-ranked; large mosses with stems arching over and rooting at tips; caps. barrel-shaped, nodding, from erect leafy shoots (acrocarpous); common (Fig. 39) 44. *Mnium*
29. Very black tufted moss on rocks; caps. covered by lvs.; teeth red, (acrocarpous) 21. *Grimmia*
29. Stems creeping, or if erect, branching freely (Fig. 40-52) 30

PLEUROCARPI

30. Main stems creeping in soil; erect shoots bushy-branched at top (2-5cm. tall) (Fig. 48) 53. *Climacium*
30. Stems not normally buried in earth 31
31. Lvs. strongly toothed, papillose at outer end of each cell 51. *Bryhnia*
31. Lvs. opaque because of papillae on cells; entire, or toothed at apex 32
31. Lvs. translucent, not papillose 37
32. Lvs. without midrib, often white-tipped; caps. covered by lvs., without operculum (acrocarpous) 22. *Hedwigia*
32. Lvs. with midrib (*Leskeaceae*) 33
33. Lvs. almost orbicular, coarsely and irregularly toothed; on oak trees (Fig. 44) 49. *Thelia*
33. Lvs. more elongate, entire or nearly so (Fig. 40-43) 34
34. Lvs. strongly papillose, slenderly acuminate, the costa ending near the middle; on trees, rare 47. *Fabroleskea*
34. Not showing the above combination of characters 35
35. Evenly pinnately branched; paraphyllia many or few (Fig. 40) 45. *Thuidium*

² *Pleuridium palustre* with caps. wholly enclosed by lvs., "along edge of canal, Upper Gar Lake", and *Amphidium californicum* with caps. projecting from lvs. "on sandy ground near Spirit Lake" are minute mosses reported by Miss Cavanagh (6).

35. Not evenly pinnate; paraphyllia rarely seen36
36. Lvs. very small, ovate, more or less acute but not hair-tipped; caps. erect; common46. *Leskea*
36. Lvs. closely appressed to stem, crowded, hair-tipped; or spreading and more or less tongue-shaped (Fig. 41-43)48. *Anomodon*
37. Lvs. with midrib (costa)38
37. Lvs. without midrib46
38. Without paraphyllia39
38. With numerous oval, toothed paraphyllia; in marshes, rare 55. *Cratoneuron*
39. In water or marshes; lvs. turned to right and left of stem, the tapered tips bent down (at least at ends of stems) (Fig. 52)54. *Drepanocladus*
39. Lvs. 2-ranked, glossy, not bent down (Fig. 51)52. *Eurhynchium*
39. Lvs. nearly equally placed around stem40
40. Very slender mosses; lvs. about 1mm. long; cells of leaf mostly rhombic41
40. Stouter; lvs. larger; cells mostly linear43
41. Lvs. close to stem or spreading; midrib straight42
41. Lvs. clearly to strongly bent back shortly above base (squamose) (Fig. 47)57. *Campylium*
42. Lvs. irregularly dentate with entire cells projecting from margin; caps. erect64. *Fabronia*
42. Lvs. nearly or quite entire; caps. curved, strongly contracted below mouth when dry58. *Amblystegium*
43. Lvs. rounded at apex; rare56. *Calliergon*
43. Lvs. pointed at apex44
44. Lvs. acuminate, very entire (Fig. 49)58. *Amblystegium*
44. Lvs. more or less toothed on margin45
45. Foliage dull or somewhat shiny; lvs. often pleated lengthwise (Fig. 50); no spur on back; beak of operculum short50. *Brachythecium*
45. Foliage glossy; little pleated, if at all; midrib ending in a spur on back of leaf; beak of operculum long52. *Eurhynchium*
46. Lvs. about 1mm. long, or less47
46. Lvs. 2-3mm. long49
46. Lvs. 3.5-7mm. long; streaming from rocks in brooks65. *Fontinalis*
47. Lvs. with straight axis, erect or spreading48
47. Lvs. squarrose (axis sharply bent back) (Fig. 47); caps. curved57. *Campylium*
47. Lvs. with sharp points all bent downward59. *Hypnum*
48. Very dark green or olive, small moss on trees and old wood; clustered buds on tips of some branches; many square alar cells; caps. erect63. *Platygyrium*
48. Very tiny mosses, the lvs. scarcely visible without a lens; few if any square alar cells61. *Amblystegiella*
49. Lvs. flat, not folded, in flat sprays (Fig. 51); margin toothed or entire; no distinct alar cells; caps. curved, inclined60. *Plagiothecium*
49. Lvs. large, shiny, entire, with distinct square alar cells; when sprays are flat, marginal lvs. folded62. *Entodon*

SYSTEMATIC LIST AND KEY TO SPECIES

Hepaticae

Marchantiales

Ricciaceae

1. RICCIA

1. In floating clusters or mats, or stranded (Fig. 1)*R. fluitans**

2. RICCIOCARPUS

1. With a fringe of scales beneath when floating; in shallow water, or stranded (Fig. 2)*R. natans**

Marchantiaceae

3. CONOCEPHALUM

1. Thallus 1-1.5cm. wide; aromatic when bruised (Fig. 5).
.....*C. conicum**

4. MARCHANTIA

1. With umbrella-shaped erect reproductive shoots; pores oval (Fig. 3, 4)*M. polymorpha**

5. PREISSIA

1. On cool rock faces; pores round (Fig. 6, 8)*P. quadrata*

6. REBOULLIA

1. Thallus 4-6mm. wide; porous under a lens (fig. 9)
.....*R. hemisphaerica**

Jungermanniales

Metzgeriaceae

7. ANEURA

1. Thallus 10-12 cells thick at middle (fig. 10)*A. pinguis**

8. PELLIA

1. Thalli about 8mm. wide; species unknown*

Jungermanniaceae

9. FRULLANIA (Figs. 12, 13, 16)

1. Autoicous (antheridia and archegonia on same plant)
.....*F. inflata**

1. Dioicous (on different plants) *F. bolanderi**

10. PORELLA

1. Underlobes narrower than underleaves, tapering to apex (Fig. 11) *P. platyphylla**

11. PLAGIOCHILA

1. Leaf margins slightly bent down, upper surface convex
..... *P. asplenoides**

12. LOPHOCOLEA

1. Lvs. 1mm. wide, some of them entire (Fig. 14, 15, 17)
..... *L. heterophylla**
1. Lvs. much smaller, deeply notched, with 1-celled gemmae at tips (Fig. 18) *L. minor**

13. JUNGERMANNIA

1. Leafy stems about 1mm. wide, scattered or in mats (Fig. 19)
..... *J. sphaerocarpa*

Anthocerotales

Anthocerotaceae

14. ANTHOCEROS

1. Spores yellow, with finely granular surface (Fig. 20) *A. laevis**

Musci

Bryales

Nematodontae

Polytrichaceae

15. POLYTRICHUM (Fig. 21)

1. Lamellae covered by transparent leaf margins 2
1. Lamellae uncovered; margins toothed (Fig. 22) 3
2. Leaf ending abruptly in a colorless hair *P. piliferum*
2. Leaf tapering to a colored point *P. juniperinum**
3. Terminal cell of lamellae notched; caps. nearly cubical (Fig. 22)
..... *P. commune*
3. Terminal cell of lamellae rounded, not enlarged; caps. much longer than broad *P. gracile*

16. CATHARINEA

1. Lamellae covering $\frac{1}{3}$ to $\frac{1}{4}$ of width of leaf. (Fig. 23)
..... *C. angustata**
1. Lamellae covering $\frac{1}{8}$ to $\frac{1}{10}$ of leaf. *C. undulata**

* Var. *alteoristata* with lamellae 5, 6-12 cells high, "on partly shaded bank on W. Okoboji Lake" is reported by Miss Cavanagh (6).

Arthrodontae**Aplolepideae****Fissidentaceae**

17. FISSIDENS (Fig. 28)

1. Stems 3cm. long; in water *F. julianus*
1. Shorter, and not in water 2
2. Lvs. bordered by narrow long cells; minute *F. incurvus**
2. Lvs. bordered by 2 or 3 rows of paler cells; large *F. cristatus**
2. Lvs. not bordered; sporophyte at end of shoot; on moist rocks
..... 3
3. Lvs. entire; operculum scarcely beaked *F. obtusifolius*
3. Lvs. finely toothed; beak long, needle-like *F. osmundioides**

Dicranaceae

18. CERATODON

1. In small or large dense sods (Fig. 38) *C. purpureus**

19. DICRANELLA

1. Seta yellowish; lvs. bent to one side (Fig. 30) *D. heteromalla**
1. Seta red; lvs. symmetric⁴ *D. varia**

20. DICRANUM

1. Caps. stout, curved; seta 2-4cm. long *D. scoparium**

Grimmiaceae

21. GRIMMIA

1. Lvs. with short hair tip or none; on boulders. *G. apocarpa**
1. Lvs. with long white hair tip; on Sioux quartzite
..... *G. poecilostoma*⁵

22. HEDWIGIA

1. More or less prostrate; with white tips *H. albicans**
1. Lacking the white tips var. *viride**

Tortulaceae

23. ASTOMUM

1. Lvs. spirally twisted when dry; caps. in autumn and early
spring *A. sullivantii**

⁴ *Dicranella rufescens* with red seta and large, thin walled, transparent leaf cells, "on seepy ground near Lower Gar Lake" is reported by Miss Cavanagh (6).

⁵ As *G. leucophaea* Grev. in Cavanagh (6), and *G. glauca* as identified by G. N. Jones.

24. WEISIA

1. Whole plant $\frac{1}{2}$ cm. tall, in little sods (Fig. 31) *W. viridula**

25. GYMNSTOMUM

1. Pale green, about 1cm. tall; not seen in fr. (Fig. 35)
..... *G. calcareum*

26. BARBULA

1. Midrib extending beyond the blunt apex of leaf *B. unguiculata**
1. Midrib ending in the gradually tapered apex *B. fallax**

27. DESMATODON

1. Plant with sporophyte about 1cm. tall, on rock faces (Fig. 24)
..... *D. arenaceus*

28. TORTULA

1. Leaf cells smooth; hair tip smooth; on earth (Fig. 26)
..... *T. mucronifolia**
1. Lvs. papillose; hair tip rough; on Sioux quartzite *T. ruralis*

Diplolepidaceae

Acrocarpae

Orthotrichaceae

29. ULOTA

1. Capsule gently tapering into seta *U. americana*

30. ORTHOTRICHUM

1. On rocks 2
1. On trees (Fig. 27) 3
2. Capsule half exposed above lvs *O. porteri*
2. Capsule completely lifted above lvs., rounded abruptly to the
seta *O. anomalum*
3. Lvs. round-obtuse at apex; margins scarcely recurved; strongly
papillose *O. obtusifolium*
3. Lvs. with a minute hyaline apiculus *O. schimperi**

Funariaceae

31. APHANORHEGMA

1. On muddy shores, in open clusters *A. serratum**

32. PHYSCOMITRIUM

1. Seta 5-15mm. long; lvs. serrate above (Fig. 29) *P. turbinatum**
1. Seta scarcely longer than lvs.; lvs. nearly entire *P. hookeri**

33. FUNARIA

1. Seta 2-4cm. tall, bent and twisted (Fig. 32) *F. hygrometrica**

Timmiaceae

34. TIMMIA

1. Calyptra erect at bend of seta (Fig. 34) *T. cucullata**

Aulacomniaceae

35. AULACOMNIUM

1. 1-4 cm. tall, pale green, in tufts; very rare *A. palustre**

Bartramiaceae

36. PHILONOTIS

1. Stems red, darker below; rare *P. fontana**

37. BARTRAMIA

1. In soft cushions 5-20cm. across, 3-5cm. tall (Fig. 25)
..... *B. pomiformis**

Bryaceae

38. LEPTOBRYUM

1. Plant about 3cm. tall; caps. thin walled *L. pyriforme**

39. POHLIA

1. Plant 3-4cm. tall; caps. thick walled *P. nutans**

40. MNIOBRYUM

1. Pale green, watery moss; not seen fruiting *M. albicans**

41. BRYUM (Fig. 33, 36)

1. Lvs. strongly decurrent; in wet places *B. bimum**
1. Lvs. not decurrent 2
2. Tiny matted silvery moss of dry places; lvs. not bordered
..... *B. argenteum**⁶
2. Larger, green; lvs. bordered by narrow cells 3
3. Cilia lacking or rudimentary 6
3. Cilia present, appendiculate (Fig. 36i); seta curved but not
the caps. (Fig. 33) 4

⁶ *B. argenteum lanatum*, white hairy with hair-like leaf tips, occurs on Sioux Quartzite.

4. Costa long excurrent 5
4. Costa percurrent or shortly excurrent *B. capillare**
5. Dioicous (antheridia and archegonia on different plants)
..... *B. caespiticium**
5. Synoicous (antheridia and archegonia in same cluster)
..... *B. intermedium*
6. Caps. curved; inner peristome nearly free from outer; teeth
simply cross-barred *B. uliginosum**⁷
6. Caps. symmetrical; inner peristome firmly adhering to outer;
teeth with vertical and oblique bars on inner face *B. pendulum**⁸

42. ANOMOBRYUM

1. In small sods, or rising singly among liverworts
..... *A. filiforme americanum*

43. RHODOBRYUM

1. Mostly in sods 5-30cm. across (Fig. 37) *R. roseum (ontariense)**

44. MNIMUM

1. Lvs. without marginal teeth; large *M. affine rugicum**
1. Lvs. with single teeth on margin 2
1. Lvs. with teeth in pairs *M. marginatum**
2. Teeth on upper half of leaf only; very common (Fig. 39)
..... *M. cuspidatum**
2. Teeth all around, of 2-3 cells each *M. affine ciliare**

Pleurocarpi

Leskeaceae

45. THUIDIUM

1. Apical cell of branch leaf papillose; paraphyllia very numerous
on stem (Fig. 40 l, p) 2
1. Apical cell of branch leaf not papillose *T. microphyllum**
2. Branching closely pinnate; branches tapering *T. abietinum*
2. Branching bipinnate, "fern-like" (Fig. 40s) 3
3. Stem lvs. erect-spreading when moist, gradually tapering to
apex; perichaetial lvs. ciliate *T. delicatulum**
3. Stem lvs. recurved-spreading when moist, abruptly narrowed to
apex; perichaetial lvs. not ciliate *T. recognitum**

⁷ Also identified as *B. pallens* and *B. inclinatum*, we think wrongly so (H. S.C.)

⁸ Formerly reported as *B. inclinatum*.

46. LESKEA

1. Lvs. more than 2x as long as wide, acute to acuminate 2
1. Lvs. less than 2x as long as wide, acute to obtuse 3
2. Capsule straight, erect *L. polycarpa**
2. Capsule curved, but erect *var. paludosa**
3. Lvs. symmetric, with a pleat on each half; margins often recurved; the commonest tree moss *L. gracilescens**
3. Lvs. unsymmetric, not pleated; margins plane *L. obscura**

47. FABROLESKEA

1. Small, dark colored, loosely spreading *F. austinii**

48. ANOMODON

1. Lvs. ending in a hair point (Fig. 43) *A. rostratus**
1. Lvs. more or less tongue-shaped 2
2. Midrib ending well below the rounded apex of lf. (Fig. 41)
..... *A. minor**
2. Midrib nearly touching apex; lvs. with a tiny point and sometimes a few teeth at tip (Fig. 42) *A. attenuatus**

49. THELIA

1. Light green; julaceous; papillae forked (Fig. 44)
..... *T. asprella**

Hypnaceae

50. BRACHYTHECIUM*

1. Lvs. strongly pleated lengthways (Fig. 50) 2
1. Lvs. not pleated, or only slightly so when dry 5
2. Lvs. very strongly pleated (Fig. 50); alar cells small, cubical; caps. nearly erect; very common *B. oxycladon**
2. Lvs. less plicate; caps. inclined to horizontal 3
3. Stem lvs. broadly triangular-ovate; cubical alar cells very numerous *B. digastrum**
3. Stem lvs. ovate-lanceolate, acuminate; basal cells broad, distinct 4
3. Stem lvs. lanceolate, gradually and evenly tapering from base to apex *B. flexicaule**
4. Seta smooth *B. salebrosum**
4. Seta rough above *B. campestre**

* See figures in Grout: Mosses with hand lens and microscope, the differences in cell details being quite indescribable.

5. Lvs. evenly tapering from base to apex, the margin a straight line; seta smooth; common in bogs *B. acutum**
5. Lvs. with curved margins 6
6. Mostly on trees; seta smooth; caps. erect, straight 7
6. Mostly on soil or rocks or in water; caps. curved 8
7. Larger; cells elongate *B. acuminatum**
7. Smaller; cells rhombic, 4-8:1 *B. cyrtophyllum**
8. Small, in thin mats, clinging closely; seta rough above
..... *B. plumosum**
8. Large, stout, sometimes bushy; seta rough throughout 9
9. In or near water; lvs. strongly decurrent, the alar cells enlarged and inflated *B. rivulare**
9. In rich woods; lvs. slightly decurrent, without peculiar alar cells *B. rutabulum**

51. BRYHNIA

1. Lvs. 1mm. long or less; in delicate green sods .. *B. graminicolor**

52. EURHYNCHIUM

1. Lvs. 2-ranked; apical cells of leaf not peculiar *E. serrulatum**
1. Lvs. all round stem; apical cells broad and short 2
2. Lvs. broadly ovate; seta rough *E. hians**
2. Branch lvs. lanceolate, blunt; stem lvs. broadly ovate, abruptly short-acuminate; seta smooth *E. strigosum robustum**

53. CLIMACIUM

1. Base of leaf auriculate-cordate; cells 5-7 times longer than wide (Fig. 48) *C. americanum**
1. Base of leaf simply cordate; cells 10:1 *C. dendroides*

54. DREPANOCLADUS

1. Lvs. strongly falcate-secund; no enlarged alar cells (Fig. 52) 2
1. Lvs. falcate-secund or not so; with a cluster of inflated alar cells (Fig. 46) 3
2. Plant reddish; lvs. with long slender acumination (Fig. 52); cells very long and narrow, 10-30:1, 0.006mm, wide
..... *D. revolvens**
2. Plant green to yellowish; acumination and cells of leaf shorter
..... *D. intermedius**
3. Alar cells colorless, thin walled; costa slender *D. aduncus* 4

3. Alar cells colored, thick walled; costa stout; robust land form with crowded falcate lvs. *D. sendteneri*¹⁰
4. Lower leaf cells linear 5
4. Lower leaf cells oblong-hexagonal *D. a. polycarpus* 7
5. Stem lvs. falcate-secund, channeled at apex *D. a. typicus* 6
5. Stem lvs. flat, straight (except at tips of stems), lanceolate
..... *D. a. kneiffii intermedius**
6. Lvs. 3-4mm. long, with long slender falcate acumination
..... *D. a. t. aquaticus**
6. Lvs. lanceolate; cells narrowly linear, flexuose; auricles of inflated cells very large *D. a. t. pseudofluitans*
7. Stems mostly creeping or floating 8
7. Stems erect, stout, in large sods (Fig. 46) *D. a. p. uncus*
8. Lvs. with long slender acumination, falcate; aquatic
..... *D. a. p. aquaticus*
8. Lvs. with acumination about $\frac{1}{2}$ the length of the rest of the leaf; aquatic *D. a. p. filicuspis*
5. Lvs. strongly secund, with short channeled acumen; on earth
..... *D. a. p. gracilescens*¹¹

55. CRATONEURON

1. Costa percurrent; cells 3-6:1 *C. filicinum**

56. CALLIERGON

1. Stems green; in wet places *C. cuspidatum**
1. Stems red; in mesic woods *C. Schreberi**

57. CAMPYLUM

1. Midrib distinct; lvs. gradually acuminate (Fig. 47)
..... *C. chrysophyllum**
1. Midrib absent, or very short, or double 2
2. Very slender; alar cells not enlarged; on dry ground or wood
..... *C. hispidulum**
2. Stouter; alar cells inflated; basal cells thick walled, porose; in bogs, often erect *C. stellatum**

58. AMBLYSTEGIUM¹²

1. Midrib very stout, extending into apex or beyond; in or near water (Fig. 45, 49) 2

¹⁰ Also forma *gracilescens*¹¹ Also subform *tenuis*¹² See figures in Grout: Mosses with hand lens and microscope, the differences in cell details being quite indescribable.

1. Midrib ending near middle of leaf, or above 3
2. Stem lvs. cordate-ovate, acuminate (Fig. 49) *A. irriguum**
2. Stem lvs. cordate-ovate, acute or obtuse (Fig. 45)
..... *A. orthocladon**¹³
2. Stem lvs. lance-ovate, with slender acumen
..... *A. fluviale brevifolium*
3. Median cells rhomboid, 8:1 or wider 5
3. Median cells long and slender, 10:1 or narrower
..... *A. riparium* 4
4. On earth or rotten wood; cells very slender *A. r. typicum**
4. Stems long, soft, streaming in water *A. r. fluitans**
5. Costa very feeble; cells short and broad; lvs. less than 1mm.
long 6
5. Costa very strong for size of leaf; lvs. less than 1mm. long
..... *A. varium**
5. Costa of medium strength; lvs. 1mm. or more long 7
6. Lvs. pressed close to stem when dry; on old wood or bark
..... *A. serpens**¹⁴
6. Lvs. spreading when dry *A. juratzkanum**
7. Lvs. slightly toothed on margin; cells 4-6:1 8
7. Lvs. very entire; cells 6-8:1 9
8. Midrib reaching into base of acumination *A. trichopodium**
8. Midrib ending about middle of leaf *A. t. kochii**
9. Lvs. broadly ovate, shortly acuminate *A. brevipes*
9. Lvs. lance-ovate, acuminate *A. riparium laxirete**

59. HYPNUM

1. Dark green, in dense thin mats *H. reptile**

60. PLAGIOTHECIUM

1. Lvs. serrate nearly or quite to base (Fig. 51) *P. deplanatum**
1. Lvs. entire, or rarely denticulate at apex *P. denticulatum**

61. AMBLYSTEGIELLA

1. Thin closely attached films on rocks or bark *A. adnata**

62. ENTODON

1. Shoots cylindric *E. seductrix**¹⁵
1. Shoots very flat *E. cladorrhizans**

¹³ A form with shorter costa in var. *brevinerve*.

¹⁴ A very slender form is var. *tenue**

¹⁵ Var. *minor*, "lvs., seta and capsule shorter than in type", "at base of bur oak, near Lower Gar Lake" is reported by Cavanagh (6).

63. PLATYGYRIUM

1. In dense mats 5mm. thick *P. repens**

Fabroniaceae

64. FABRONIA

1. Fine film on Cedar tree bark *F. octoblepharis*

Fontinalaceae

65. FONTINALIS

1. Lvs. distant, loosely spreading *F. lesurii**

Species, varieties and forms in the key

Hepaticae	16
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Musci	128
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	144
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In footnotes, from Cavanagh	6
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Total	150
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Known from Emmet County

Hepaticae	14
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Musci	100
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	114
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EXPLANATION OF TERMS USED IN THE KEY

acumen, a tapering leaf tip whose margins are concave; hence acuminate (Fig. 43, 44, 47, 49)

alar cells, the cells at the basal-marginal angles of a leaf (Fig. 46)

apiculus, a little abrupt point on a rounded leaf tip (Fig. 24)

appendiculate, with knobs or short bars at intervals (Fig. 36, 1)

auriculate, bowed out like ears (Fig. 48, 1)

autoicous, archegonia and antheridia on separate shoots from the same plant

cordate, notched or heart shaped

costa, a midrib of a leaf; costate, with a costa

crenate, with coarse rounded teeth

decurrent, margins of leaf continued down along stem

dentate, with coarse teeth sloping equally toward base and apex of leaf

denticulate, finely dentate

excurrent, protruding beyond the lamina

falcate, curved, sickle shaped (Fig. 46, 52)

flagelliform, long and slender, whip-like

flexuose, wavy and winding

gemma, a 1- or few-celled propagating body

hyaline, clear, transparent

incubous, arranged like shingles on a roof if base of plant is at ridge and apex at eaves (Fig. 11, 12)

julaceous, cylindrical and smooth or downy

lamina, the flat green part of a leaf

lanceolate, about 4 times as long as wide, broadest near base and tapering to a point

mesic, of a moist habitat, neither very wet nor very dry

orbicular, nearly circular

ovate, egg-shaped in outline

papilla, a tiny lump or knob on a cell wall; hence papillose (Fig. 24, 32)

paraphyllia, thread-like or tiny leaf-like growths on a stem (Fig. 40p)

percurrent, of a costa that runs clear to the tip of a leaf (Fig. 25, 31)

perichaetial, around base of seta

porose, of thick walls with thin spots (pores)

recurved, bent backward (downward)

revolute, rolled backward more closely than recurved (Fig. 37, 1)

secund, all turned to one side, usually downward (Fig. 52)

serrate, saw-toothed

sessile, without any stalk

squarrose, spreading and recurved (Fig. 47)

succubous, arranged like shingles on a roof if base of plant is at eaves and apex at ridge (Fig. 14, 19)

underleaf, a small leaf on the under side of stem (Fig. 11, 12)

underlobe, a lobe of the leaf folded under and lying close to the leaf (Fig. 11, 12)

EXPLANATION OF PLATES

Figures of Hepaticae are mostly from drawings by Miss Esther Collette; figures of Musci are by Miss Mary Perry. This help is gratefully acknowledged by the authors.

Plate I

1. *Bicia fluitans*, entire plant, nat. size.
2. *Ricciocarpus natans*, floating form with ventral scales, and with capsules in midrib; nat. size.
3. *Marchantia polymorpha*, showing antheridial receptacles, gemma cup and at a marginal scales on ventral side, and median ventral scales; nat. size.
4. *Marchantia polymorpha*, archegonial receptacle, nat. size.
5. Receptacle of *Conocephalum conicum*, with one perianth projecting from under side; nat. size.
6. Receptacle of *Preissia quadrata* seen from above showing 4 thalloid areas with pores; x 1.5.
7. Polygonal areas of thallus with an air pore in each area, x 4.
8. Ventral-median scale of *Preissia*, x 10.
9. Ventral-median scale of *Reboulia*, x 10.
10. Thallus of *Aneura pinguis*, nat. size.
11. *Porella platyphylla* seen from beneath, showing underleaves (central row) and underlobes; x 10.
12. *Frullania* from beneath, showing underleaves and underlobes, x 20.
13. Perianth of *Frullania*, seen from above, with tubular opening and two dorsal ridges; x 15.
14. *Lophocolea heterophylla*, with terminal perianth; x 12.
15. Unopened capsule of *Lophocolea heterophylla*, x 12.
16. Elater from capsule of *Frullania*, x 50.
17. Elater from capsule of *Lophocolea heterophylla*, x 50.
18. Leaf of *Lophocolea minor* with gemmae, x 12.
19. *Jungermannia sphaerocarpa*, seen from the side, x 5.
20. *Anthoceros laevis*. Sporophytes rising from their perianths, the larger one split in two (dehiscence), showing columella; nat. size.
21. *Polytrichum juniperinum*; teeth of peristome (nematodontous), x 20.
22. *P. commune*; trans. sec. leaf, showing lamellae, x 20.
23. *Catharina angustata*; a, cross section, b, entire leaf, x 15 and 10.
24. *Desmatodon arenaceus*; a, b, leaf tips; c, peristome; x 20.
25. *Bartramia pomiformis*; a, top of plant with sporophyte; b, leaf; x 5.
26. *Tortula mucronifolia*, peristome, x 15.
27. *Orthotrichum*, with "immersed" capsule, x 5.
28. *Fissidens* leaf, split on one side near base, x 15.
29. *Physcomitrium turbinatum*, x 5.
30. *Dicranella heteromalla*, capsule with arthrodontous teeth, x 10.
31. *Weisia viridula* leaf seen from above (margins involute), and cross sections of leaf at different levels, x 15.
32. *Funaria hygrometrica*, capsule, x 10.
33. *Bryum* capsule, nodding, pear-shaped, x 10.
34. *Timmia oviculata*, capsule and calyptra, x 10.
35. *Gymnostomum calcareum*; a, leaf; b, leaf apex; c, cells from middle of leaf.

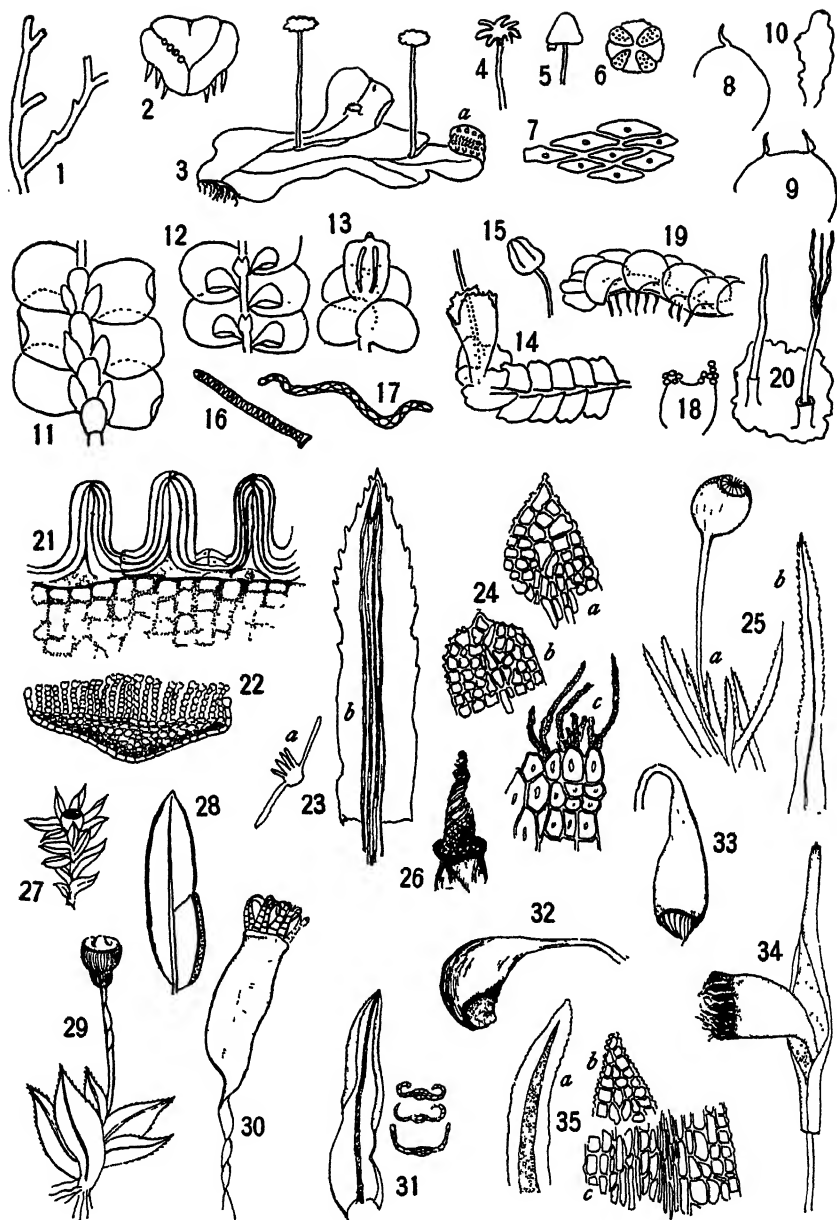
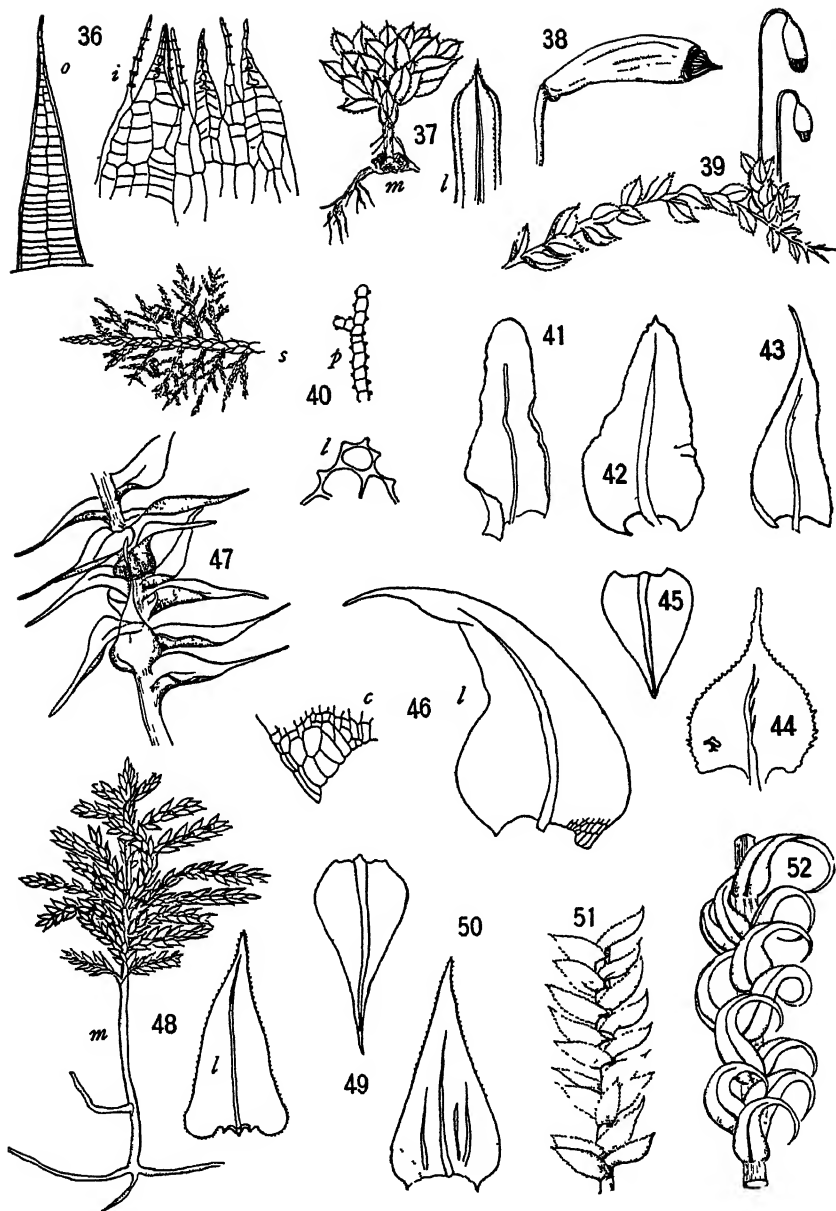


Plate II

36. *Bryum intermedium*; *o*, tooth of outer peristome; *i*, teeth (segments) and appendiculate cilia of inner peristome; x 65.
37. *Rhodobryum roseum (ontariense)*; *m*, mature plant, nat. size; *l*, leaf from beneath with revolute margins, x 3.
38. *Ceratodon purpureus*, capsule, x 12.
39. *Mnium cuspidatum*, creeping and erect shoots, x 3.
40. *Thuidium delicatulum*; *s*, a shoot bipinnately branched, nat. size; *p*, paraphyllium; *l*, apical cell of branch leaf with 3 papillae, x 50.
41. *Anomodon minor* leaf, x 15.
42. *A. attenuatus* leaf, x 15.
43. *A. rostratus* leaf, x 20.
44. *Thelia asprella* leaf, x 20; *a* forked papilla much enlarged.
45. *Amblystegium orthocladon* leaf, x 15.
46. *Drepanocladus aduncus polycarpus unicus* Grout; *l*, leaf, x 20; *o*, alar cells, x 50.
47. *Campylium chrysophyllum* with squarrose leaves, x 15.
48. *Climacium americanum*; *m*, plant nat. size; *l*, leaf, x 12.
49. *Amblystegium irriguum* leaf, x 15.
50. *Brachythecium oxycladon* leaf with longitudinal pleats, x 15.
51. *Plagiothecium deplanatum*, showing flat spray, x 5.
52. *Drepanocladus revolvens*, stem and leaves, x 5.

PLATE II



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A COMPARATIVE MORPHOLOGICAL STUDY OF THE MYXOMYCETE FRUCTIFICATION

by

GLADYS E. BAKER

A COMPARATIVE MORPHOLOGICAL STUDY OF THE MYXOMYCETE FRUCTIFICATION

GLADYS E. BAKER

Morphological studies of slime molds have consisted mainly of taxonomic investigations and developmental studies. External characters have been used in taxonomy as well as those internal characters which are readily seen by microscopic examination of the sporangia. The early workers in the field based their classifications primarily on external appearances. DeBary (1, 2, 3) was the first to emphasize microscopic details. Rostafinski in his monograph revolutionized the system by using almost entirely internal characters as the basic principles of his classification. Later both external and internal characters were correlated in taxonomic descriptions, as in the works of Lister (7) and Macbride (8).

Rostafinski followed closely the work of DeBary, his teacher. His *Sluzowce* (10) is beautifully and profusely illustrated. Among his figures is a fair proportion of diagrams of the internal structure of sporangia. In many cases, though finely executed, these do not include sufficient detail to be of value except for purposes of general orientation. Of those illustrations that do attempt to show clearly the internal relations, many are inaccurate. These drawings were not made directly from sections, but were reconstructions, which would account for such inaccuracies.

Massee (9) also includes several illustrations of fructifications in section, but his figures are of even less value. Lister and Macbride chiefly illustrate external views, spores, and capillitial characters. To such figures as are found in these books reference will be made later.

Very few authors have included diagrams of sections of mature forms. The purpose of this work has been to show as nearly as possible the nature and the exact relations of the chief structures of the mature sporangia, such as the walls, capillitium, columella, and stalk. Spore characters have not been considered. Sixty-four species representing thirty-three genera have been studied. Both Lister and Macbride have been followed for generic and specific

descriptions. With a few exceptions, Macbride's synonymy and classification have been accepted.

Material for the work was taken largely from the mycological herbarium of the State University of Iowa. The collections range in age from one to twenty-five years. Unfortunately, many collections in the herbarium do not have complete collection data—in many instances, especially, the date is omitted. However, the majority of the material used was collected within the last five years. It was supplemented by several collections of fresh material made in the fall of 1931 near Iowa City. Sections of *Badhamia rubiginosa* (Chev.) Rost. were cut from a 1928 herbarium collection and from sporangia killed in Bouin's fluid in the fall of 1931. No essential differences between the two were noted. Dried material gave results as satisfactory as those obtained with fresh specimens.

All studies were made from sections cut in paraffin, with additional whole mounts whenever necessary. The earlier sections made from herbarium collections were first soaked in 95% ethyl alcohol, swelled in a dilute solution of potassium hydroxide, washed, and dehydrated by a butyl alcohol series, using the grades recommended by Zirkle (12). Later, it was found more satisfactory to put the sporangia on moist filter paper in covered petri dishes, where they were left over night. In this way no potassium hydroxide was used, the sporangia being transferred directly to the first of the butyl series. Sections from material treated by the second method preserved to a greater extent the wall and external calcareous deposits. All slides were stained by a short triple method—safranin, crystal violet, and aqueous orange G. Measurements of spores from sporangia dehydrated in both ways were within Lister's or Macbride's limits.

Sporangia collected in the field were killed in Bouin's fluid for twenty-four hours, washed and dehydrated in the same way as the herbarium material. Sections cut twenty microns thick proved the most satisfactory, especially for capillitial characters.

As it was found impractical to make the drawings on a common scale, the magnifications are given for each. All drawings were made directly with a Zeiss microscope and a camera lucida, with the exception of figures 1, 4a, 27a, 42, 43, 44, and 56, which were reduced to suitable sizes from camera lucida originals. The drawings included here are representative of sporangia in the particular collections used. Undoubtedly, there is a great deal of variation,

particularly in size, form, and amount of lime present, in different collections of the same species. An effort was made to select collections which were typical of the species. Though at times the diagrams of different species are remarkably similar or structurally very simple, yet the drawings are presented to afford correlation of the essential characters. No attempt has been made to discuss generic characters. For each species a description of its characters and a drawing or more when needed, have been included.

It has been impossible to achieve conclusive results concerning the nature of the aethalioid forms, except in the case of *Dictydiaethalium plumbeum* (Schum.) Rost., for which several young stages of material were available. It is hoped that all the so-called aethalioid slime molds will be studied in their entire development to determine their exact form.

The types of fructifications are defined according to the conceptions of Martin. These include: the aethalium—hypothetically the most primitive form, in which all or a considerable part of a given plasmodium is involved, and in which differentiation has not proceeded to the delimitation of separate sporangia; the pseudo-aethalium—in which the sporangia are delimited, but borne in compact and more or less attached groups; the plasmodiocarp—approaching the sporangiate type and formed of the principal veins of the plasmodium; the sporangium—the typical erect fructification representing only part of the plasmodium.

This study was suggested by Professor G. W. Martin and completed under his direction in the mycological laboratory of the State University of Iowa.

The list of species studied is as follows:

PHYSARALES

PHYSARACEAE

1. *Fuligo septica* (L.) Gmelin
2. *Fuligo muscorum* Alb. and Schw.
3. *Badhamia macrocarpa* (Ces.) Rost.
4. *Badhamia utricularis* (Bull.) Berk.
5. *Badhamia rubiginosa* (Chev.) Rost.
6. *Physarum serpula* Morgan
7. *Physarum lateritium* (Berk. and Rav.) Morgan
8. *Physarum sinuosum* (Bull.) Weinm. ex Fr.
9. *Physarum cinereum* (Batsch) Pers.

10. *Physarum melleum* (Berk. and Br.) Massee
11. *Physarum citrinum* Schum.
12. *Physarum globuliferum* (Bull.) Pers.
13. *Physarum penetrans* Rex
14. *Physarum nucleatum* Rex
15. *Physarum didermoides* (Ach.) Rost.
16. *Physarum compressum* Alb. and Schw.
17. *Physarum flavicomum* Berk.
18. *Physarum gyrosum* Rost.
19. *Physarum polycephalum* Schw.
20. *Craterium leucocephalum* (Pers.) Ditm.
21. *Craterium leucocephalum* var. *scyphoides* Lister
22. *Craterium minutum* (Leers) Fries
23. *Physarella oblonga* (Berk. and Curt.) Morgan
24. *Leocarpus fragilis* (Dickson) Rost.
25. *Cienkowskia reticulata* (Alb. and Schw.) Rost.

DIDYMIACEAE

26. *Mucilago spongiosa* (Leyss.) Morgan
27. *Didymium squamulosum* (Alb. and Schw.) Fries
28. *Didymium minus* Morgan
29. *Diderma radiatum* (L.) Morgan
30. *Diderma spumarioides* Fries
31. *Lepidoderma tigrinum* (Schröd.) Rost.
32. *Colloderma oculatum* (Lipp.) G. Lister

STEMONITALES

33. *Stemonitis fusca* Roth
34. *Stemonitis axifera* (Bull.) Macbride
35. *Comatricha nigra* (Pers.) Schroet.
36. *Comatricha suksdorfii* Ellis and Everh.
37. *Diachaea cerifera* G. Lister
38. *Diachaea leucopodia* (Bull.) Rost.
39. *Enerthenema papillatum* (Pers.) Rost.
40. *Enerthenema melanospermum* Macbride and Martin
41. *Lamproderma violaceum* (Fries) Rost.
42. *Lamproderma arcyrionema* Rost.

CRIBRARIALES

43. *Licea biforis* Morgan
44. *Licea minima* Fries
45. *Licea variabilis* Schrad.
46. *Lindbladia effusa* (Ehr.) Rost.
47. *Tubifera ferruginosa* (Batsch) Gmelin
48. *Enteridium splendens* (Morgan) Macbride
49. *Dictydiaethalium plumbeum* (Schum.) Rost.
50. *Cribraria argillacea* Pers.

LYCOGALES

51. *Lycogala epidendrum* (L.) Fries

TRICHIALES

52. *Margarita metallica* (Berk. and Br.) Lister
53. *Listerella paradoxa* Jahn
54. *Ophiotheca wrightii* Berk. and Curt.
55. *Ophiotheca vermicularis* (Schw.) Massee
56. *Perichaena depressa* Libert
57. *Arcyria globosa* Schw.
58. *Arcyria denudata* (L.) Wettstein
59. *Arcyria cinerea* (Bull.) Pers.
60. *Hemitrichia vesparium* (Batsch) Macbride
61. *Hemitrichia serpula* (Scop.) Rost.
62. *Hemitrichia clavata* (Pers.) Rost.
63. *Trichia varia* Pers.
64. *Oligonema nitens* (Libert) Rost.

Fuligo septica (L.) Gmelin. Figs. 4a, 4b.

The aethalial fructification of *Fuligo septica* is usually large and pulvinate. Its wall is membranous and rugose, with numerous calcareous deposits throughout, but especially abundant laterally and basally. Within are spores and capillitium. The latter consists of many membranous knots, some quite decidedly calcareous, others not, but all more or less connected by fine threads.

It has been customary to refer to this slime mold as an aethalium. On the basis of Martin's terminology it is an aethalium, but in an opposite sense from standard definitions. There is no evidence in sections of mature specimens that the membranous expansions

represent vestigial sporangia. More probably they represent pseudo-capillitium formed as the result of degenerating protoplasm.

Of published illustrations of this species, Rostafinski's deserve the first consideration. Figure 97 in his monograph presents a view of the central stratum of the aethalium, showing the vein-like protoplasmic areas characterizing its development. Figs. 101 and 104 show equally well the separate details of the capillitium. But his diagram of a median section, fig. 106, achieves scarcely more than location of the different layers of the fructification. Massee has a meaningless diagram of such a section, but neither Lister nor Macbride illustrates the species in this way.

Fuligo muscorum Alb. and Schw. Fig. 1.

Fuligo muscorum forms irregular fructifications that are pulvinate or elongate in habit. An individual fructification consists of interwoven tubes, often regarded as sporangia, but more probably representing vein-like regions of the plasmodium or closely combined plasmodiocarps. A single membranous wall bearing some lime fuses basally with the delicate membranous hypothallus. Besides the internal walls, a true capillitium of lime nodes and short threads is present.

It is perhaps justifiable to regard this form as an aethalium, at least until more definite results are obtained. The only illustrations of the species are in Lister's *Monograph*.

Figure 1 represents a median vertical section.

Badhamia macrocarpa (Ces.) Rost. Fig. 2.

Sessile, subglobular sporangia are typical of this *Badhamia*. Its single, somewhat rugulose wall is membranous, with here and there lime inclusions. The capillitium is not entirely badhamioid, but in part approaches the physaroid type, for its calcareous tubes and knots are often connected by short, fine threads.

Only external appearance, spores, and capillitium have been illustrated by Massee and Rostafinski. Lister has an excellent series of this type, but Macbride has no drawings of the species.

A view of a section cut through an entire sporangium is given here.

Badhamia utricularis (Bull.) Berk. Fig. 5.

The sporangia of this species are subglobular and in contrast with those of the preceding species are large and stipitate. A very

delicate membrane serves as the peridium. On its exterior are numerous calcium granules, usually quite round and marked with radial striae. Small clumps of calcium granules are scattered in the wall at intervals. A weak, slender, fibrous stalk—its edges roughened by loose ends, and about two-thirds the sporangium height—supports the sporangium. There is no hypothallus. The capillitium is moderately broad, flattened, and expanded at the axils. Occasionally fine threads connect larger knots. Its arrangement is not intricate: it simply forms a uniform network in the interior. The spores often remain in clumps of three or more, or are entirely free, depending upon the particular sporangium.

Rostafinski and Lister illustrate the capillitial and growth characters in an excellent series of drawings. Neither Massee nor Macbride made drawings for this species.

Badhamia rubiginosa (Chev.) Rost. Fig. 6.

This species, clearly a *Badhamia*, has a definite stipe rising from a discoid hypothallus. Its sporangia are obovoid, bounded by heavy membranous walls which are confluent with the walls of the columellae and the stalks. The fusiform columella, a continuation of the stalk, attains three-fourths of the sporangium height, becoming broadest about one-third below its apex. Both columella and stalk are filled with lime granules. The capillitium is a rugged network of broad tubes, densely charged with lime and extending from columella to wall.

Badhamia rubiginosa is of common occurrence, yet in the standard works on slime molds one usually finds illustrated only gross characters and separate details. Rostafinski attempted a median view of a sporangium, but his figure is quite inaccurate.

Figure 6 is an internal view of a mature sporangium, showing the relations and structure of the wall, columella, and capillitium.

Physarum serpula Morgan. Figs. 8a, 8b.

This is a plasmodiocarpous form that is terete in section. The wall is membranous and filled with irregularly distributed lenticular lime granules which take a heavy stain. The capillitium is abundant, almost badhamioid, consisting of large irregular knots and bands, connected by short, fine threads. The capillitial knots contain lime granules, though less profusely than the wall.

The specific nature of these granules is not emphasized in the literature. However, Lister's illustration of the capillitium and

wall suggests their presence. Macbride's description of the capillitium as "charged with polygonal nodules of lime" probably refers to these granules, though they are decidedly not polygonal. When a portion of a sporangium is mounted on a slide, the granules appear perfectly clear, with a slight yellowish cast.

Physarum lateritium (Berk. and Rav.) Morgan. Fig. 3.

The sporangia of the collection studied are sessile and subglobose. The single, thin, rugulose membrane that forms the peridium has occasional calcium granules in its outer edge. At the base the wall is somewhat thickened, forming a more or less distinct hypothallus. Internally, the capillitium forms a close net of fine threads and rounded calcareous knots of varying size and shape.

Although this species is easily separated from *P. cinereum* by color, and by character and size of spores, the distinctive differences in their internal morphology are very slight. The nodes of *P. cinereum* are a bit more angular than those of *P. lateritium*.

Physarum sinuosum (Bull.) Weinm. ex Fr. Fig. 15.

Short plasmodiocarps or distinct sessile sporangia are found in this *Physarum*. The particular sporangia sectioned are laterally compressed, varying little in width from base to apex, a character that is typical though not constant. There is a double wall, the outer layer of which is broad and rough, breaking irregularly at the apex for dehiscence. Apically it is thicker and covers the spore mass after the outermost part has split. The inner layer is a membrane of variable width to which the capillitium is attached. The capillitium is a freely branching system of large lime knots and slender short threads.

In Rostafinski's monograph, Plate V, fig. 91, there is an illustration of the species in section. It is not altogether accurate, but it is the best diagram in the literature. The basal portion of the sporangium is least correct; in all the sections examined the walls are continuous at the base. Masee has a small sketch which suggests only the manner of dehiscence.

Physarum cinereum (Batsch) Pers. Fig. 17.

This very simple, sessile, subglobose fructification is borne on a hypothallus. The sporangial wall is fine and membranous with

heavy calcareous deposits at intervals on the outside. Typically physaroid capillitium extends throughout the sporangium.

For all practical purposes, this species is adequately illustrated in Lister. A diagram of structure simply enables one to correlate its internal and external characters at a glance.

Physarum melleum (Berk. and Br.) Massee. Fig. 9.

This species is representative of the columellate *Physarums*. The sporangia are globose on a stalk that is about equal in height to the sporangium. A thin membrane forms the peridium, becoming confluent at the base with the wall of the stalk. The columella is a conical extension of the stalk. Both stalk and columella are finely vesicular, almost cellular in appearance. The capillitium consists of delicate hyaline threads originating along the entire length of the columella, sometimes expanded at the axils or connected with large angular lime knots.

No essential differences between this species and *Physarum citrinum* were revealed by this method of study. However, there are several characters which quite definitely separate the two for taxonomic purposes.

Physarum citrinum Schum. Fig. 10.

Short, stout stipes bear the subglobose sporangia of *Physarum citrinum*. The single membrane of the peridium, relatively thin, is often coated on the outside with calcareous deposits. The stalk appears cellular in section, due to many fine interlacing membranes. A short tapering extension of the stalk within the sporangium serves as the columella from which the capillitium arises. The latter consists of slender straight threads and lime knots of various sizes and shapes.

This species is distinguished from *Physarum melleum* chiefly by reason of its yellow stipe. In their morphological make-up the two species are quite similar. Neither species is adequately illustrated for structure. Lister has excellent views of habit; neither Rostafinski nor Macbride illustrates it; Massee has a habit sketch of *P. citrinum*. The diagrams given here emphasize the similarities in these *Physarums*.

Physarum globuliferum (Bull.) Pers. Fig. 12.

The sporangia are globular, erected on long slender stalks, two-thirds the total height of the fructification. Inside the sporangium,

the stalk forms the short, conical columella. Varying amounts of lime are clustered on the surface of the sporangium. The sporangium wall is a single membrane, so thin that little remains after sectioning, especially when dried material is used. This membrane is confluent with the stalk. The stalk itself is composed of a homogeneous matrix surrounded by a membranous wall, and containing calcareous deposits, these granular or at times clearly crystalline. In some sporangia this deposit of calcium is very abundant, occurring in dense clumps from the base of the stalk to the sporangium, but apparently not in the columella. When a stalk is placed in weak hydrochloric acid, the lime dissolves, leaving the horny or membranous matrix. The capillitium is comparatively lime free. Though there are occasional lime filled knots, many are limeless; all knots are connected by fine threads.

Rostafinski, fig. 86, diagrams the internal structure in a manner that implies that the stalk and columella are completely calcareous.

Figure 12 is typical of conditions in the various sporangia of a herbarium collection determined by Macbride.

Physarum penetrale Rex. Fig. 19.

This *Physarum* is very similar in its structural plan to *P. globuliferum*. The sporangia, in this form, are ellipsoidal, standing on long slender stalks, two-thirds the total height. The single wall is limeless, in contrast with that of the preceding species, though there may be a few calcareous deposits. Inside, the conical columella extends two-thirds the height of the sporangium, then broadens apically. Capillitium arises along the entire columella and radiates to the wall. It consists of slender threads with scattered lime knots and triangular axillary expansions.

Lister's illustrations of the species are the only ones in recent works. Her figure b, plate 36, which was designed to show internal structure, is not clear enough to show detail.

Figure 19 is drawn from sections cut from a 1926 collection of Brandza's, typical except that the particular sporangium drawn is somewhat flattened rather than oval.

Physarum nucleatum Rex. Fig. 7.

Physarum nucleatum is so named from the presence of a central mass of lime. Typically the fructification consists of a slender, solid stalk, a little more than half the total height, and a sub-

globose sporangium, bearing some lime on the outside. In the center is the large mass of lime from which the close capillitial net of fine threads and scattered lime knots radiates.

Only one author, Lister, illustrates this species. Her figures are beautifully drawn and the detailed drawing of the "nucleus" and capillitium shows clearly enough their relation to each other.

Physarum didermoides (Ach.) Rost. Fig. 14.

The sporangia of this *Physarum* are ovoid and shortly stalked. Their walls are composed of three layers: the outermost a heavy calcareous shell, most of which is destroyed in sectioning; a middle, delicate membrane to which the calcareous layer is attached; and a heavy membrane on the inside, that at times is closely combined with the middle membrane or may be widely separated. Short, delicate, membranous stalks support the sporangia, which may be more or less united in groups. In the center of each sporangium there is a large mass of lime bounded by a membrane of variable thickness. It is supported by very fine threads with numerous rounded lime nodes which radiate throughout the sporangium.

Rostafinski has a splendid drawing of the species in section, though his material apparently lacked the central lime mass. The character of the wall appears two-fold in contrast with the three layers described here. Macbride states that if the calcareous cap is present, the central lime mass is lacking. Both were clearly present in the material used.

Physarum compressum Alb. and Schw. Fig. 13.

Fan-shaped sporangia, the result of lateral compression, are characteristic of the stipitate forms of *P. compressum*. Sections were cut parallel to the flattened surface and also at right angles to it. As no fundamental differences were apparent only the former section is illustrated. The wall is membranous, bearing closely adhering lime granules on the exterior. The stout, somewhat furrowed stalk is coarsely granular in section, and encrusted on the outside with lime. A network of fine short threads and variously shaped lime knots is typical of the capillitium, which is attached on all sides.

In Rostafinski's monograph there is a clear-cut sectional diagram. The character of the stalk is too regular and there is a suggestion

of a columella, but aside from that it leaves nothing to be desired. No other sectional drawings of this species were found.

Physarum flavicomum Berk. Figs. 11a, 11b.

Nodding, slightly flattened sporangia are borne on tall slender stalks free from calcareous deposits. The walls are single membranes with inclusions of pellet-shaped bodies in the region of the stalks. These stain red with safranin and are irregularly distributed, as are the lenticular granules in *P. serpula*, but in this species they are larger. At times they are present in the upper part of the stalk. The capillitium is a simple net of threads with axillary expansions and small angular lime knots.

Figure 88 in Rostafinski illustrates very nicely the general plan of this species, though the sporangium is not complete. There is nothing in it to indicate the presence or nature of the curious granules mentioned above.

Physarum gyrosum Rost. Fig. 18.

According to Macbride's classification, this is one of the *Physarums* in the Tilmadoche group. The sporangia are massed, labyrinthine and fused, forming almost an aethalioid mass on a common hypothallus. Their walls are simple and non-calcareous. Within, the capillitium, consisting of extremely fine threads with large fusiform lime nodes, is oriented transversely to the walls.

No illustrations besides Lister's very excellent series were found. This, however, does not include a sectional view.

Physarum polycephalum Schw. Fig. 16.

The sporangia of *Physarum polycephalum* are gyrose and dichotomously lobed. There is a fine capillitium with calcareous nodes here and there through the sporangial head. The stalk is membranous with an internal granular deposit, non-calcareous. There is no membrane separating it from the sporangium. The wall is membranous and in this case with little calcium, owing probably to the fact that the sporangia used were matured in a moist chamber.

A life history of this species has been worked out by Howard (5). It is interesting to note from his work that there is no membrane between sporangium and stalk at any stage, and that the fructification is not compound in that all the lobes are continuous with the central portion, even though by very small openings.

Craterium leucocephalum (Pers.) Ditm. Fig. 25.

The small, obovoid, stalked sporangia of *Craterium leucocephalum* open by irregular circumscission. The outer layer of the double wall is slightly thinner in the upper portion, and membranous with a few lime granules in vesicular pouches. Some lime is free on the surface. The inner wall is a thin membrane. At the base the walls are thicker, almost cartilaginous. The cartilaginous stalk, from a small hypothallus, is confluent with the outer wall. In the center of the sporangium there is a pseudo-columella of aggregated lime granules, unevenly distributed and bounded by a fine membrane. It is supported by the capillitium of fine branching threads interspersed with moderate sized lime granules.

Massee illustrates a median vertical section of this, but it is not accurate. No lime occurs in the stalk as there indicated; the threads are too heavy; and the columella is unlike any seen in the present study. Excellent habit sketches are included in both Rostafinski and Lister.

Craterium leucocephalum var. *scyphoides* Lister was studied but there is so little difference between the typical species and this variety that the variety was not illustrated.

Craterium minutum (Leers) Fries. Figs. 22, 23, 24.

Sporangia from three different collections were sectioned. The first, a Brandza collection (No. 41, August 1927), is characterized by goblet-shaped, stalked sporangia (fig. 23). Dehiscence is by a regular lid, not inserted but dome-shaped. The lid itself is thinner than the sporangium wall. There are occasional lime deposits on the inner side of the peridium. The stalk is thick and confluent with the wall. No pseudo-columella is present, but the lime knots of the capillitium are very large and irregular.

An Oregon collection made by M. E. Peck has short, broad sporangia that are almost fan-shaped in section (fig. 22). The wall is double—the inner, a calcareous layer; the outer, membranous merging into cartilaginous at the junction with the stalk. There are the same layers in the lid, but it is thinner and bears crystalline lime nodules on the outside and in the wall itself. The lime knots are smaller than in the preceding specimen, but there is no pseudo-columella.

Another collection reveals the typical *C. minutum* form with inserted lid (fig. 24). There is a much thinner calcareous inner

layer than in the sporangia of Peck's collection, though it is undoubtedly present on the inner side of the membranous layer. The outer wall of the sporangium and the wall of the stalk are distinct at the base of the sporangium, but merge farther up. The stalk is cartilaginous. A true lid, more or less calcareous, is present. It is depressed with a prominently projecting rim. The capillitium consists of small lime knots and fine threads. In the center the lime unites to form a pseudo-columella.

Rostafinski's illustration of this species is beautifully drawn, but highly diagrammatic. The internal character is correct, but the wall is too schematic to be of scientific value. According to his diagram, there are three layers in the wall—the outer seemingly cartilaginous; a more or less calcareous middle layer; and an innermost membrane to which the capillitium is attached. Such a wall was not found in any of the material studied. All three variations described are illustrated.

Physarella oblonga (Berk. and Curt.) Morgan. Fig. 21.

This slime mold has cylindrical stipitate sporangia that are hollow from apex to base. The wall is membranous and single. On the interior it forms the spurious columella which is continuous with the hollow stalk. The inner and outer walls fuse at the base of the sporangium to form the wall of the stalk. Filiform capillitium, rarely forking, extends from the inner to the outer wall. Trabeculae, stout calcareous bands, have broad attachments on the outer wall. A few continue directly across to the interior wall, but the majority taper to a fine point and are connected with the inner wall by short threads. The trabeculae are persistent on the outer wall when the sporangium opens.

Rostafinski, Appendix, figure 243, has illustrated a median vertical section in an entirely satisfactory way. Other authors contribute necessary details and habit views.

Cienkowskia reticulata (Alb. and Schw.) Rost. Fig. 26.

Plasmodiocarpous in habit, this species is attached to its substratum by a narrow base. The single wall is membranous and free from lime except at the points of attachment of the calcareous plates which are at right angles to the axis of the fructification. The capillitium is a loose network of fine threads with numerous

free, pointed, and curved ends. These threads are connected at times with the calcareous plates.

No diagram of internal morphology was found. Figure 26 represents a plasmodiocarp sectioned at right angles to the plates.

Leocarpus fragilis (Dickson) Rost. Fig. 20.

Sporangia from two different collections were sectioned, but only one illustrated as there were no differences other than size and shape. The sporangia are large, obovoid and stipitate. There are three layers in the wall. The outer layer is thick, cartilaginous, and brittle, so that in sectioning it may split in a shingle-like fashion. It is continuous with the stalk. Innermost is a membrane to which the capillitium is attached. Between this membrane and the cartilaginous layer, there is a heavy amorphous calcareous deposit. The stalk is very slender, filiform, and weak, rising from a hypothallus common to several sporangia. The capillitial element is double—one system of very fine threads with the majority of its nodes limeless and another of large calcareous tubes. Both occur in all parts of the sporangium and are occasionally connected, though more often quite distinct.

There is a good drawing of the wall with capillitium attached in Rostafinski, figure 93.

Mucilago spongiosa (Leyss.) Morgan. Figs. 27a, 27b.

The fructification of this species is aethalioid, composed of labyrinthine tubes with membranous walls, the whole interspersed with calcareous deposits. A broad cortex of calcium crystals surrounds the outside. These are for the most part densely clustered along fine membranes which originate from the apical ends of the sporangium-like veins and form a loose reticular cortex. A similar arrangement, though not so extensively developed, is found at the bottom. Internally, the calcium crystals are especially aggregated along the walls. A spongy hypothallus connects the entire fructification with the substratum.

Figures 27a and 27b are drawn from vertical sections.

Didymium squamulosum (Alb. and Schw.) Fries. Fig. 30.

The stalked sporangia of this species when sectioned make particularly fine slides. They are hemispherical, deeply umbilicate beneath, and on the exterior are covered with crystals, most of

which are stellate, though a few are flattened. The wall is a single membrane of varying thickness. The deeply furrowed and channelled stalk is heavily coated with lime nodules both inside and outside. At the base it is confluent with the hypothallus. A vesicular expansion at the top of the stalk, filled parietally with lime granules, forms the columella. Slender, flexuose threads, the capillitium, radiate from wall to wall. The character of the stalk varies, for in some specimens it is not so deeply furrowed nor so heavily lime crusted.

Massee has a small illustration which does not adequately suggest internal structure. In Rostafinski there is a well drawn series, yet it is inaccurate for the character of the stalk and columella.

Didymium minus Morgan. Fig. 33.

The sporangia of *D. minus* are hemispherical and umbilicate like those of *D. squamulosum*, but their stalks are four-fifths the entire height, solid and cartilaginous. The columella is a vesicular expansion filled with lime granules and a few fine membranous threads. The capillitium of sparingly branched, flexuose threads, reaches from the columella to the inner wall. Some threads that are decidedly larger than the others branch to form small ones.

Rostafinski's unexcelled illustration of *D. farinaceum* (synonymous with *D. melanospermum*) shows a very similar structure.

Diderma spumarioides Fries. Fig. 29.

Sessile, hemispherical sporangia, umbilicate beneath, characterize the fructification. The wall is double, composed of an outer calcareous crust and fine inner membrane. A membranous, convex columella with its numerous membranes giving it a cellular appearance is continuous with the stalk, which is constitutionally the same. There may be occasional deposits of lime granules in both. The slender branching threads of the capillitium radiate from columella to wall. There may be a calcareous layer on the upper surface of the hypothallus, which is continuous among many sporangia.

Rostafinski depicts a series of sporangia of this species with their hypothallus and columellae heavily encrusted with lime. Such a decidedly calcareous condition was not found in any of the material used, though it may occur, of course.

Diderma radiatum (L.) Morgan. Figs. 31a, 31b.

From a Colorado collection, sections were cut of sporangia ranging from stalked to almost sessile forms. A true double wall was not found, the typical case apparently consisting of outer and inner membranes enclosing a homogeneous, amorphous, calcareous mass. As these are so closely combined and almost indistinguishable at times, it seems doubtful to interpret this as a three-fold wall. The stalk, when present, is stout, membranous, becoming cartilaginous near the base. There are occasional calcium deposits in it. Columella and stalk are continuous, the former a convex expansion of the stalk. The capillitium is sparingly branched, flexuose, and attached to the inner membrane and wall.

Some specimens seem to lack the outermost membrane, in which case the wall could perhaps be called double.

There are illustrations of this species in section in Rostafinski, but they are morphologically inaccurate.

Lepidoderma tigrinum (Schräd.) Rost. Fig. 28.

This handsome slime mold has large hemispherical sporangia, deeply umbilicate, on stout furrowed stalks, two-thirds the total height. The wall is single, cartilaginous and covered with large granules or scales of calcium. A few of these scales are covered by membranes, but the majority are free. In section, the stalk is reticulate and vesicular, with crystals of calcium in the lacunae. The columella, as in other Didymiaceae, is an expansion of the stalk. Its furrows are much smaller and the lime nodules more numerous than in the stalk. Typical capillitium radiates abundantly from wall to wall. On close examination the calcium scales are seen to be closely appressed, not firmly embedded. In early stages it is possible that they are covered by very fine membranes.

Figure 159, Rostafinski, is the best median sectional view in the literature, though it is not correct for the structure of the columella.

Figure 28 was drawn from a Washington specimen collected by Macbride.

Colloderma oculatum (Lipp.) G. Lister. Fig. 32.

Unlike any other slime mold, the sporangia of *Colloderma oculatum* are encased in a heavy gelatinous sheath which forms the outer wall of the fructification. In places it has heavy granular deposits. Within this sheath, the usually sessile spore mass is en-

closed by a single membrane which is very delicate. The sporangia are ellipsoidal or subglobose with flattened bases from which the capillitium arises. This consists of branching, anastomosing, straight threads, slenderer near the surface.

Lister supplies the only illustrations of the species.

Figure 32 shows a median vertical section.

Stemonitis fusca Roth. Fig. 40.

Characteristically the sporangia of this species are cylindrical, obtuse at both ends, slender, and stalked. The stalk, slender and about one-fourth the total height, comes from a small hypothallus. At the extremity of the columella—a continuation of the stalk within the sporangium—several primary branches of the capillitium are given off. The network of capillitium extends from the columella to the surface by primary branches which anastomose and gradually become finer to form a peripheral net with angled meshes.

Criticisms of the illustrations of this species in Massee, Lister, and Macbride, would be much the same as those mentioned in connection with the following species

Stemonitis axifera (Bull.) Macbride. Fig. 41.

Sporangia of this species are exceedingly long and slender with slightly acuminate apices. The slender stalk, which rises from a hypothallus, is about one-third the entire height and is continued within the sporangium as a columella. In the sporangium, the columella extends nearly to the apex. Larger primary horizontal branches connect with a fine angular peripheral net. There are many free ends on the surface by which the wall, early evanescent, is supposedly supported.

Lister does not recognize this species as *S. axifera* but as *S. ferruginea* Ehrenb. Massee also refers to it under that specific name. This however, is merely a matter of synonymy. Massee includes among his illustrations a bit of the net from the columella to the surface, but the primary branches seem too heavy in proportion to the peripheral net and the transition between the two too abrupt. Lister's figure showing the same structure is confusing as it represents the entire body. A diagram of a median longitudinal section is of greater value in orientation. One would scarcely be able to separate *S. axifera* and *S. fusca* on the basis of the illustrations of the capillitial net in Macbride.

Comatricha nigra (Pers.) Schroet. Fig. 36.

The globose, somewhat flattened sporangia of the collection used stand on solid tapering slender stalks about three times the sporangium height. At times there is a continuous hypothallus among the sporangia. The stalk is continued within the sporangium about three-fourths of its height. It gradually tapers and divides almost directly into the finer surface network through a few intermediate heavy branches. Heavy primary threads proceed horizontally from the columella, branching and anastomosing to form the finer surface network. The net is dense only at the surface. There are a few free ends resembling short barbs on the outside.

DeBary (2) has a good illustration of the species, although a view of a section would be less confusing than an illustration of an entire sporangium such as he has drawn.

Comatricha suksdorfii Ellis and Everh. Fig. 39.

In this form the sporangia are large, cylindrical, and obtuse at both ends. A short, rather stout stipe rises from a small hypothallus. For a short distance the stipe is latticed in a manner similar to that of some Lamprodermas. The columella extends nearly to the apex of the sporangium, where it expands into a membranous web-shaped structure from which heavy capillitial threads originate, or simply divides into several main threads as in *C. nigra*. The capillitium is a very dense network attached along the length of the columella. The primary branches are heavy, but soon anastomose and branch throughout the sporangium. The entire net is closer than that of *C. nigra*, in which the main branches are quite conspicuous. At the outside there are many free ends, pointed, long and slender.

In distinguishing between *Comatricha suksdorfii* and *Comatricha nigra*, the gross characters such as the size, shape of the sporangium, and length of the stalk, are the most outstanding. Of the detailed characters the numerous free ends of the network of *C. suksdorfii* and their size and shape are significant, as is also the dense, closely branched net. It does not seem probable that a distinction could be made on the basis of the columellae for there seem to be no constant differences for that character.

Of the illustrations of *C. nigra* in extant works, Lister's are good for growth habits; Rostafinski's series is suggestive of sporangial variation; Macbride has a good picture of the structural

character in its entirety. For *C. suksdorfii*, also, Macbride offers the best figures.

Diachaea cerifera G. Lister. Fig. 38.

This interesting slime mold is stipitate, with subglobose sporangia which often have large waxy collars at their base. These collars, which resemble a huge cushion in section, are of a rough heterogeneous nature with a smooth outer layer. The entire structure takes a heavy stain with crystal violet. The single, delicate sporangium wall merges at the base into the collar. With the collar the stalk is over one-half the total height. It originates as a slender stalk and gradually expands to meet the collar with which it is confluent. Rigid, straight threads, comprising the capillitium, extend from the base to the walls in a fan-like manner. There is some branching. At the points of attachment to the wall, both above and below, the threads often become abruptly finer.

Lister gives the only description and illustration of the species. As usual, she includes splendid habit views and detailed drawings of capillitium and spores, but nothing to indicate its general construction.

Diachaea leucopodia (Bull.) Rost. Fig. 35.

The ovoid, obtuse sporangia are bounded by single, very thin, membranous walls. They are borne on stalks, one-third the total height of the fructification, which are lime filled and bounded by a thin membrane. The columella is a continuation of the stalk, also lime filled, extending well into the sporangium. Fine threads comprise the capillitium that radiates from the columella to the peridium. The nodes are limeless. At the points of attachment to the columella and peridium the threads are finer, especially at the peridium.

This genus is clearly differentiated from the two preceding genera by the characteristic limy stalk and the persistent peridium. It is allied to them by the capillitium, which sometimes forms a net to support the wall. Lister classifies the genus with the Physaraceae between the Physarums and Didymiums and suggests that it may be a connecting link between the Calcarineae and Stemonitaceae.

Massee illustrates and describes *D. leucopodia*, but gives no figures aside from habit and spores. He places the genus among

the Didymieae. Macbride has no illustrations of this species. Lister's figures give an adequate representation of its separate characters. Two partly opened sporangia in figure a, plate 99, show general internal construction. Rostafinski's figure 178 is the nearest approach to the diagrammatic representation of the internal structure. But, as in Lister's drawing, the result would be more satisfactory if only a section of the sporangium were shown.

Enerthenema papillatum (Pers.) Rost. Fig. 37.

One of the determining characters of this genus is the delicate membranous peridium which persists for only a short distance around the apical concave disc.* The stalks of the globular sporangia are about equal to the sporangium height. In section the stalk is latticed from the hypothallus to the origin of the columella. The solid columella is merely an extension of the stalk within the sporangium. It tapers gradually to the apex, then expands again to form the disc from which all the capillitium originates. Its long flexuose threads extend downward with some branching; they are free in mature specimens.

Rostafinski does not include this species among those illustrated in his monograph, but Masee, Macbride, and Lister all have satisfactory pictures of it.

Enerthenema melanospermum Macbride and Martin. Fig. 34.

This species is strikingly larger than *E. papillatum*, although it resembles it in many ways. As in the smaller species the sporangia are globular, have a thin membranous wall, persisting only apically, and are stalked. However, at the point of origin of the sporangium wall the stalk is expanded in a large node. Stalk, node, and columella are all continuous. The very large apical disc bears the capillitium.

There are no important differences between this and *E. papillatum* as shown in section, except size and the presence of the large node at the junction of stalk and wall.

Lamproderma arcyronema Rost. Fig. 48.

The globose sporangia of this form have a delicate persistent membrane. The stalk, about equal in height to the sporangium, is latticed internally. Within the sporangium, the columella ex-

tends practically half way. At its apex it divides into several primary branches from which smaller capillitial threads lead off. These threads are freely branched and anastomose to form a round-meshed net, with some free ends. There seem to be no attachments to the peridium. It is interesting to note that the stalk is latticed condition not readily seen in gross examinations.

Lamproderma violaceum (Fries) Rost. Fig. 49.

This species has many characters in common with the preceding one. Though the stalk is longer than in *L. arcyryonema*, it is structurally the same. At the junction of the sporangium and stalk, on each side of the columella and between it and the wall, there is a comparatively large, membranous area. This may be peculiar to the collection studied, though the sporangia appear otherwise normal. The capillitium arises from the apical region of the columella and for some distance along it. The net is made up of straight smooth threads, anastomosing and branching, and forming a close surface net. Its ends are mostly free and quite fine at the tips.

There are few figures of these two species. In Rostafinski, there is a small diagram of *L. violaceum*, figure 64, indicating the extent of the columella and the origin of the capillitium from it; he does not illustrate *L. arcyryonema*. Massee drew the same species, but not to any great advantage. On the other hand, Macbride illustrates *L. arcyryonema* with the wall entirely removed; this does not give a complete picture of the structure. Both are represented in Lister, but the results are rather confusing as the entire sporangia are drawn. These *Lamprodermas* retain their walls well enough to justify their illustration and description in such a stage.

Licea variabilis Schrad. Fig. 47.

Typically this is a large, sessile, pulvinate form without a hypothallus. Its lack of capillitium is characteristic of the genus as a whole. In this species there is a double wall—the outer layer thick, rough, and cartilaginous; the inner thin, delicate and membranous. Dehiscence is irregular.

In the literature this species is often described as *L. flexuosa*, as in Massee and Lister. Lister does not recognize the presence of two walls, but prepared sections confirm Macbride's observations of a double wall. The rough outer layer is closely appressed to

the thin inner membrane. It is more or less deciduous and is, therefore, often lacking in places.

No illustrations representing structure were found.

Licea minima Fries. Fig. 45.

A Colorado collection furnished the material for the study of this species. Its sessile, hemispherical sporangia are small and have no hypothallus. A single thick, cartilaginous wall opens by one or more predetermined lobes. The "peg-like warts" as described by Lister, are clearly visible on the inner sides of the lobes in the upper portions of the sporangium, but they do not occur on the lateral walls or along the base. They are pendant, like stalactites, and in places are abundant.

Licea biforis Morgan. Figs. 46a, 46b.

The fusiform sporangia of *L. biforis* are extremely small. There is a comparatively thick wall which opens by a longitudinal fissure at the top. Lister's comparison to a "date-stone" is apt. In section the lobes of dehiscence are tapered but rather blunt at the margins. Within the sporangium, the spores exhibit a regular radial arrangement. This shows to best advantage in section, for it can hardly be determined by an entire mount.

The walls of *L. minima* and *L. biforis* are very similar. Lister calls the former cartilaginous and the latter membranous. Again (6) he described the wall of *L. biforis* as similar to that of *L. flexuosa*, though with fewer external deposits. Judging from sections made from a collection of Morgan's, this is incorrect. When Lister's definition of cartilaginous is applied to these species as seen in section, both are apparently cartilaginous.

Illustrations of these species in Lister are sufficient for habit and detail. The sectional diagrams shown here illustrate more clearly the exact manner of dehiscence.

Lindbladia effusa (Ehr.) Rost. Figs. 42, 56.

A Pennsylvania collection of the species shows individual sporangia that are short stipitate. There is but a single layer of them, mostly free, though at times several are closely compressed. Short, rugulose stalks connect the sporangia with the well-developed hypothallus. The outer and innermost layers of the hypothallus are

thickened. The thin membranous walls of the sporangia are confluent with the stalks.

In another collection, from Nebraska, (no. xxvi), the sporangia are superimposed in several layers, forming a pulvinate pseudo-aethalium. The whole structure rests upon a membranous hypothallus. The sporangia are cylindrical, though often much compressed. As in the former collection, the walls are membranous, with scattered, very fine plasmodic granules which take a clear red stain with safranin. It is possible to distinguish the individual walls of the sporangia even when they are closely appressed.

These two collections are suggestive of the extremes of variation in the genus and species. The sporangial forms resemble *Tubifera*; the plasmodic granules in the walls ally *L. effusa* to the *Cribrarias*, though it has no net.

Nothing can be determined from Macbride's picture, plate 12, figures 1 and 2. Lister has a good sectional view. Massee and Rostafinski have no illustrations of the species.

Tubifera ferruginosa (Batsch) Gmelin. Fig. 43.

This is a pulvinate pseudoaethalium with crowded cylindrical sporangia, more or less angled by pressure. Several layers of sporangia are superimposed upon each other. The walls of the individual sporangia are distinct, though tightly appressed in the inside areas. A heavier wall, common to all sporangia, bounds the exterior. The whole is borne on a loose, spongy hypothallus.

Macbride's illustrations are of no help, and Lister's are good only for habit and general orientation. Massee's also are unsatisfactory; Rostafinski does not illustrate the species.

Enteridium splendens (Morgan) Macbride. Fig. 44.

This pulvinate fructification is seated on a well developed hypothallus. It is bounded by a rather heavy wall or cortex, which merges basally with the hypothallus.

Internally, the whole mass is pierced by many membranous irregular bands that are expanded at the angles and at their junction with the cortex. These bands have been regarded as the walls of the numerous sporangia which make up the aethalium. Studies of mature forms give no basis for such a conclusion; rather, sections of this stage suggest that the whole is a very closely combined group of numerous plasmodial veins whose walls form the bands.

Both Macbride and Lister have regarded this form as closely related to Reticularia. Wilson and Cadman (11) after a thorough cytological and morphological study, concluded that Reticularia was not an aethalium, as no evidence of sporangial walls appeared. They termed it a sporangium that had become partially septate. This idea seems slightly far-fetched, for if it is a sporangium the bands within should develop in a fashion similar to capillitium. By their own account these are not the product of secretions but the result of protoplasmic degeneration during development and after meiosis.

On the basis of Martin's terminology, Enteridium is an aethalium and not a pseudoaethalium—(the latter term is comparable to the aethalium of Wilson and Cadman). If the bands in Enteridium are formed of protoplasmic remnants they may be regarded as pseudo-capillitium.

None of the illustrations in extant works give entirely satisfactory representations of internal structure.

Dictydiaethalium plumbeum (Schum.) Rost. Figs. 57-62.

A mature fructification of this species is pulvinate, although much flattened, on a membranous hypothallus. It is composed of cylindrical sporangia so compressed as commonly to become hexagonal, but often pentagonal or quadrangular. From the material available, young and mature stages of several different collections were studied. These gave evidence for the following points:

For each sporangium there is a membranous wall which is early evanescent. These are so closely appressed that they appear as one save at the corners. The sporangia may be four, five, six, or rarely seven sided. There are as many threads present as there are sides to a sporangium. They lie to the inside of the membranous walls and in cross-section they appear shield-shaped with the less arcuate side joined with the wall. This characteristic shape is seen in both young and mature stages, though in the latter the wall has disappeared. In longitudinal sections of mature specimens, the threads are seen to bear numerous minute spines and projections.

Apically the threads are clearly confluent with the sporangial caps, but below they do not attain the base. Many threads are in actual connection at the top, but none was found in similar junctions at the base. Either they end in a bulbous expansion or they join with other threads of the same sporangium, about one-twelfth

of the way or less from the bottom. When the basal membrane is removed, soaked in 95% alcohol, cleared, and mounted, no broken ends or other indications of thread attachment are evident.

Serial sections of young material reveal that near the base the threads gradually spread apart, become elongate in section, and finally fuse. There are no threads present in the very last sections. Only at the apex can the threads be said to mark the angles. There they come very close together at the corners of the sporangia. In the longitudinal sections one sees that the membranes definitely extend the entire length of the fructification and are attached to the floor.

The sporangial walls are commonly described as vestigial and represented by threads extending from the dome-shaped apex of each sporangium to the base. From the foregoing, it is doubtful if they are really part of the wall.

In the reconstruction of the mature pseudoaethalium, such as this, several things are outstanding, but especially the regularity and symmetry of its structure. The numerous sporangial caps give rise to as many vertical threads as there are sides to a sporangium. These extend nearly to the bottom, but end by a bulbous expansion or by uniting with other threads of the same sporangium. At the base there is a membrane with small extensions at right angles to it, indicating the points of attachment of the membranous sporangium walls, early evanescent. The entire structure is filled with spores. Below is a large, membranous hypothallus.

Among extant illustrations, Rostafinski's stand first, although they are highly diagrammatic and not too accurate. His figure 25 represents the general appearance of a section of an entire pseudoaethalium, though in reality the domed apices are more closely compressed and the bases more flattened than Rostafinski has shown them to be. His figure 30 is an artificial diagram correctly illustrating the design as seen in cross-section below the apex, but not accurate in detail.

Macbride's figure showing construction is inaccurate in that the threads do not reach the base as there implied.

Lister includes among her illustrations one of the floor of the pseudoaethalium showing the bases of the sporangia, figure 152e, and one of the caps with threads attached. The former condition is seen easily when a bit of the basal membrane is torn off and mounted. The second diagram depicts some of the threads joined

at their extremities, a fact which is suggestive of the condition mentioned previously. However, one would infer from Miss Lister's description that she intended this to represent basal attachment.

There are a few illustrations in Massee, but they do not contribute to the knowledge of the structure.

Beyond doubt, the presence of definite walls in the early stages makes this a pseudoaethalium. It appears that the threads do not continue to the base, in which case the question arises as to their function and homology. It is hoped that this very interesting form with its unusually perfect symmetry will soon be studied thoroughly in its entire development.

Cribraria argillacea Pers. Fig. 53.

From a Morgan collection of 1895, sections were made of sessile, gregarious sporangia on a distinct hypothallus. A single wall was found to be continuous over the entire sporangium, heavier at the base than in the upper portion where there are small thickenings on the inner side. These probably represent the net. The wall itself is bounded by a membrane on the exterior, but the inner surface is free—a layer of rough heavy granular deposits. Aggregations of these plasmodic granules form the thickened areas. In *Lindbladia effusa* the plasmodic granules are scattered, but in this *Cribraria* they are distributed throughout in dense clusters.

Massee, Macbride, and Lister show only entire sporangia, spores, and portions of the net.

Lycogala epidendrum (L.) Fries. Figs. 50a, 50b.

Lycogala epidendrum is one of the commonest and best known of the slime molds. The fructifications are large and sessile, dehiscing irregularly at the apex. They are surrounded by a crust or cortex of two layers which retain their identity throughout, although closely compressed in the basal portions. Of the two, the inner layer is the more homogeneous. In places it is very broad and may be separated from the outer one; again it is joined by irregular strands and tubes to the outer layer. A very fine, but distinct, membrane separates it from the spore region. On the surface there are occasional protoplasmic extrusions, usually completely covered by membranes of the outer layer. In young stages, before these protoplasmic areas are definitely pushed to the outside, the nuclei appear perfectly normal. When these areas are

completely cut off, degenerating nuclei are often visible. At maturity, only rarely are nuclear remnants distinguishable in the protoplasmic extrusions. In the upper part of the wall a few vesicles or tubes were observed, but these are more frequent in the basal region. The mature fructification contains spores and capillitium. The latter arises from the outer layer of the cortex, pierces through the inner one and is continued within. It is tube-like, often quite flat, freely branched at times, long or short, usually much wrinkled, and has round free ends.

This type of fructification can be considered only an aethalium. Since it was not studied developmentally, there is no evidence to support the idea of its being a single sporangium. Subsequent studies to determine the origin of the capillitium should be undertaken to reveal the true nature of the fructification.

There are many descriptions and studies of this genus and species in the literature. As early as 1859, DeBary (1) wrote of it and illustrated his paper with remarkably accurate drawings. However, considering the figures in some of the more recent works, it is perhaps justifiable to present a diagram of a complete aethalium as it appears in section.

Margarita metallica (Berk. and Br.) Lister. Fig. 63.

Sections were cut from herbarium material of sessile, subglobose sporangia on a small hypothallus common to several fructifications. A single thin, membranous wall opens irregularly. The capillitium is composed of fine coiled threads infrequently branched and very infrequently attached. No actual attachments were distinguished in prepared material, but their presence was verified by a fresh mount.

According to Massee, who described the species as *Prototrichia chamaeleontina* but did not illustrate it, the threads are thickened at the points of attachment. Such thickenings have not been seen, and neither Lister nor Macbride refers to a similar condition. Rather, judging from Lister's illustration, plate 196, one would infer that the threads are finer at their attachments. No drawings representing the internal structure in its entirety were found in the literature.

Listerella paradoxa Jahn. Figs. 55a, 55b.

This small sessile form grows on *Cladonia*. It has a single, but

extremely heavy, membranous wall, rough with much attached refuse matter. Tapering lobes with rather blunt ends allow for dehiscence. The capillitium is definitely attached at the base, sides, and on the lobes near the opening. Near the junction with the wall the capillitium is slightly less moniliform than in the sporangium.

Miss Lister describes this species as having scanty capillitium "attached below and perhaps above." In sections made from material collected by O. Jaap, abundant capillitium was found with definite attachments near the apex, on the sides, and at the base. Miss Lister's figures show clearly the diagnostic features of habit, capillitium, and spores. The drawing of a portion of the wall, as there presented, indicates the character but not the thickness in proportion to the entire sporangium.

Ophiotheca wrightii Berk. and Curt. Fig. 69.

The plasmodiocarpous sporangia are sessile, terete, and more or less globose in section. Material collected locally was used for study. The wall consists of two layers: the outer thick, rough, granular, forming a crust; the inner smooth, thin, and subcartilaginous. There is no lime on the exterior nor is there a hypothallus. A loose network of long, sparingly branched threads with numerous large spines, constitutes the capillitium. In section no definite attachments to the wall remained, but they are easily seen when a bit of the wall is mounted separately.

Lister credits this species with two walls; if Macbride had extended to recognize this condition, he did not make it clear. Considering other forms in which two walls are acknowledged, it seems justifiable to admit the presence of two walls in this species. No structural diagrams were found in Masee, Lister, or Macbride, but several excellent drawings of habit and separate details are available in these works.

Ophiotheca vermicularis (Schw.) Macbride. Fig. 64.

In the form of growth, this species resembles *O. wrightii*—both are plasmodiocarpous, sessile, and subglobose in cross-section. A heavy granular mass bearing many beautiful, angled calcium crystals on the exterior and a fine membranous inner layer constitute the double wall. The inner membrane is papillose on the innermost surface in young sporangia, but in older sporangia this is

not so distinct. Only by mounting a portion of the wall separately could the capillitial attachments be distinguished. In all sections the capillitium was very scanty.

Macbride writes of a single wall; Massee implies the same structure; but Lister describes two walls. Median sections confirm the latter view.

Lister does not separate the genus *Ophiotheca* from the genus *Perichaena*. One of his criteria of the latter genus is the presence of double walls. Macbride separates them on gross characters and especially by the manner of dehiscence. For this study Macbride's classification has been accepted. Whether one admits one genus or two, the walls of both these species of *Ophiotheca* are double.

Perichaena depressa Libert. Fig. 51.

Many flattened, sessile sporangia, closely crowded and angled as a result of pressure, characteristically grow together. Dehiscence is by a definite lid. The wall is double. The outer layer is thick and granular without a bounding membrane on the exterior. In the upper portion it forms the lid; on the lower side, in connection with the substratum, it serves as the hypothallus. Closely connected with this outer wall, is a thin membranous layer, continuous around the entire spore mass. After the lid is lifted laterally, this membrane remains in place over the spores. The capillitium is a branching system of slightly irregular threads that approximates a net. Its attachments are mainly in the upper part of the sporangium.

Rostafinski has no illustrations of this; Massee has shown only habit and spores. A doubtful growth habit is all that Macbride contributes. Lister's habit and details, which are good in themselves, do not adequately illustrate structure, such as the nature of the lid and its relation to the rest of the sporangium.

Arcyria globosa Schw. Fig. 66.

Characteristic stipitate, globose sporangia grow usually on *Castanea* burs. Its single membranous, slightly rugose wall, evanescent above, persistent below, is confluent with the wall of the stalk. No internal membrane separates the sporangium proper from the stalk. The latter is filled with a dense mass of spore-like cells which merge into the spore content. Massee refers to these as "large, irregular, angled cells," but in the material studied they are similar to the spores themselves in shape, although much larger.

Short arms parallel to the sporangium wall may be the bases of the capillitial attachments, but as often the attachments are typical—i.e. at right angles to the wall. Attachments are mostly in the basal part of the sporangium.

Massee and Macbride place this species in the genus *Lachnobolus* chiefly on the basis of capillitial attachment by arms, but Lister and Baskerville (4) agree in retaining it among the *Arcyrias*. Certainly its internal characters, such as the presence of spore-like cells in the stalk and character of the wall, seem to ally it with the latter group.

Arcyria denudata (L.) Wettstein. Fig. 54.

Stipitate sporangia rise from a small hypothallus. The sporangia are sub-cylindrical, slightly ovate. Above the calyculus the wall is evanescent. The calyculus itself is smooth and continuous with the wall of the stalk. The stalk, three-eighths the entire height, is filled from the base to the sporangium proper with spore-like cells. These spore-like cells are larger than the true spores and contain an inconstant number of nuclei—from one to five. The capillitium, forming a spiral network, is attached to the calyculus and to the inside of the stalk. Horizontal capillitial strands occur well down in the stalk. In the stalk and near the calyculus, the capillitium is comparatively smooth. In the expanded portion of the sporangium it is marked with cogs, ridges, or spines.

The majority of drawings of this form consist of habit sketches and details of capillitium and spores. Lister's figure a, plate 174, is the nearest approach to a structural interpretation.

Arcyria cinerea (Bull.) Pers. Fig. 52.

The particular sporangia of this species which were studied were elongated and stipitate. A thin, rugulose calyculus is all that remains of the sporangium wall, which is early evanescent. Spore-like cells fill the cylindrical stalk from the base to the sporangium. The capillitium branches freely and is attached to the calyculus and the stalk. In these regions it is much smoother than in the sporangium; the peripheral threads are especially spinose.

These three species of *Arcyria* are deserving of illustration, for there are no figures in the literature adequately showing their structure. Rostafinski's diagram of *Arcyria cinerea* in median

section shows very well the location of the spore-like cells, spores and wall, but lacks the capillitial details.

Hemitrichia vesparium (Batsch) Macbride. Fig. 67.

This slime mold is fasciculate, several clavate sporangia growing on a common stalk. The outer wall, the broader of the two, widens apically into a sheath-like cap, often delicately membranous. The inner wall is a thin membrane enclosing the spores. The stipe, common to several sporangia, is loose and reticulate. In height it is a little more than that of the sporangium itself. Below, the stalk is continuous with the narrow, flattened hypothallus. Within the sporangium the capillitium is apparently free. It is twisted, spinulose, with acuminate free ends.

No illustrations depicting these characters in their relations to one another were found in reviewing the literature. The purpose of figure 67 is to show internal and external structures as they appear in a median longitudinal section.

Hemitrichia serpula (Scop.) Rost. Fig. 70.

This is one of the sessile plasmodiocarpous forms of *Hemitrichia*, with a well developed rough hypothallus. In section the sporangia range from terete to ellipsoidal. According to Macbride's observations the wall is single. Lister describes it as double, which assertion is confirmed by the slides made for this study. The outer layer is rough, granular, and the inner is membranous. They are distinct though very closely combined. The capillitium, which is made up of sparingly branched, twisting threads, is attached mainly in the basal part.

Massee has illustrated only spores and habit; Macbride has no illustrations; Lister has good sketches of habit and detailed characters.

Hemitrichia clavata (Pers.) Rost. Figs. 68a, 68b.

The sporangia of *H. clavata* range from nearly sessile, globose forms to others that are decidedly stipitate and turbinate. A single membranous wall, smooth on the exterior and papillose on the interior, is continuous with the stipe. In those forms which are well stalked the stalk may be one-third the total height and almost uniform in width from base to apex. It is filled from the base to the sporangium with spore-like cells. No internal membrane separates

the sporangial content from that of the stalk, so that their contents merge. The capillitium is a dense net with occasional free ends and many branches. In those forms with a short stipe the capillitium is attached at the base of the stalk; in those with well developed stipes it may reach the base or arise from points near the base.

This species is distinct from *H. stipitata*, which Lister includes in it. On the basis of Baskerville's descriptions, the two are clearly separate species. There is a good drawing of an expanded sporangium in Rostafinski's monograph, figure 207.

*
Trichia varia Pers. Fig. 71.

The short, stipitate or sessile, subglobose sporangia of this slime mold are characteristic of the genus. In the stipitate forms the stalk is approximately one-half the total height. Structurally, it is reticulate and of a heavy granular nature, and continuous with the spongy hypothallus which is common to several sporangia. The walls of the sporangia are single, membranous, and slightly thickened toward the base, and merge into the outer layer of the stipe. Within the sporangium there are many free short elaters with acute ends.

No illustrations of internal structure were found. Though very simple in its plan of construction, a diagram is included to show the exact arrangement of its parts.

*
Oligonema nitens (Libert) Rost. Fig. 65.

Structurally this is a simple form. Single thin membranes bound the sessile subglobose sporangia which rest directly on the substratum without a hypothallus. Internally, the sporangia are filled with spores and short elaters which are entirely free.

Numerous illustrations of habit, spores, and elaters are available, but none representing the complete internal appearance has been found.

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PLATE I

- Fig. 1. *Fuligo muscorum* Alb. and Schw. Section of an aethalium. x 7.
- Fig. 2. *Badhamia macrocarpa* (Ces.) Rost. Section of a sporangium. x 48.
- Fig. 3. *Physarum lateritium* (Berk. and Rav.) Morgan. Section of a sporangium. x 48.
- Fig. 4. *Fuligo septica* (L.) Gmelin. a. Section of an aethalium. x 7.
b. Detail of lateral wall at the base, showing the heavy calcareous deposits. x 68.
- Fig. 5. *Badhamia utricularis* (Bull.) Berk. Section of a sporangium. x 60.
- Fig. 6. *Badhamia rubiginosa* (Chev.) Rost. Section of a sporangium. x 60.
- Fig. 7. *Physarum nucleatum* Rex. Section of a sporangium. x 48.
- Fig. 8. *Physarum serpula* Morgan. a. Section of a plasmodiocarp. x 68.
b. Detail of wall and capillitium. x 512.

PLATE I

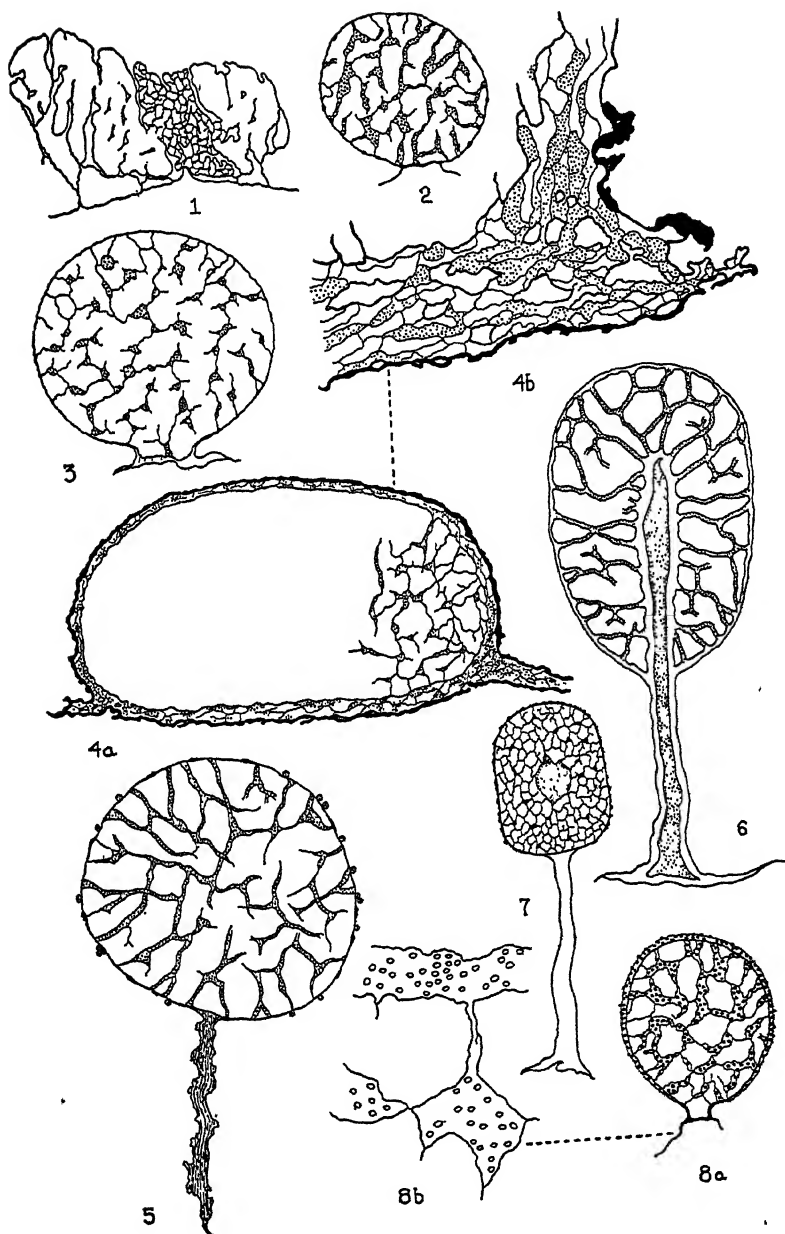


PLATE III

- Fig. 20. *Leocarpus fragilis* (Dickson) Bost. Section of a sporangium. x 30.
- Fig. 21. *Physarella oblonga* (Berk. and Curt.) Morgan. Section of a sporangium. x 48.
- Fig. 22. *Craterium minutum* (Leers) Fries. Section of a sporangium from a Peck collection. x 60.
- Fig. 23. *Craterium minutum* (Leers) Fries. Section of a sporangium from a Brandza collection. x 60.
- Fig. 24. *Craterium minutum* (Leers) Fries. Section of a typical sporangium. x 60.
- Fig. 25. *Craterium leucocephalum* (Pers.) Ditm. Section of a sporangium. x 60.

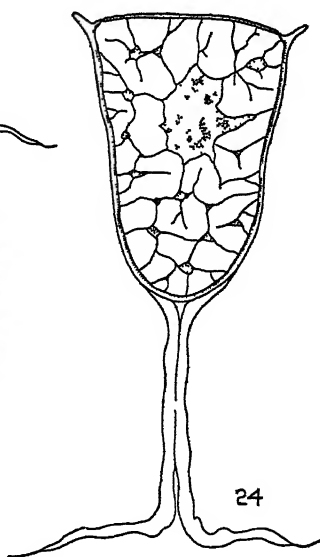
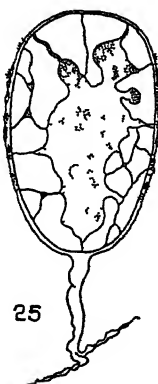
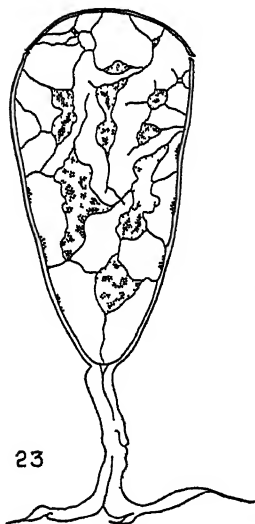
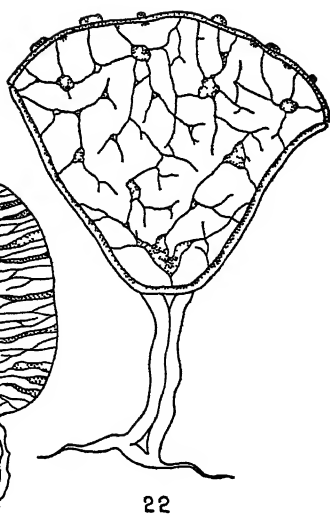
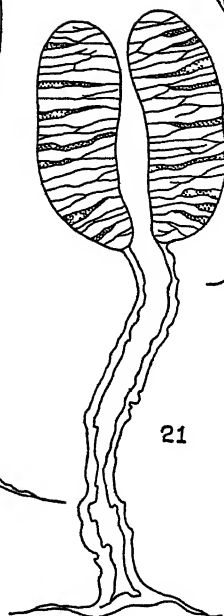
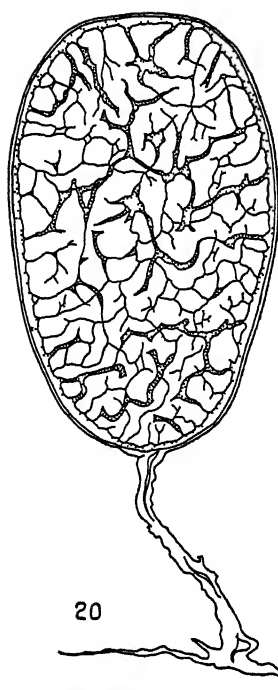


PLATE IV

- Fig. 26. *Crenkowskia reticulata* (Alb. and Schw.) Rost. Section of a plasmodiocarp. $\times 48$.
- Fig. 27. *Mucilago spongiosa* (Leyss.) Morgan. a. Section of an aethalium. $\times 2$. b. Detail of section. $\times 15$.
- Fig. 28. *Lepidoderma tigrinum* (Schrad.) Rost. Section of a sporangium. $\times 30$.
- Fig. 29. *Diderma spumarioides* Fries. Section of a sporangium. $\times 30$.
- Fig. 30. *Didymium squamulosum* (Alb. and Schw.) Fries. Section of a sporangium. $\times 30$.
- Fig. 31. *Diderma radiatum* (L.) Morgan. a and b. Sections of sporangia showing variation in form. $\times 30$.
- Fig. 32. *Colloclerma oculatum* (Lipp.) G Lister. Section of a sporangium. $\times 48$.
- Fig. 33. *Didymium minus* Morgan. Section of a sporangium. $\times 48$.

PLATE IV

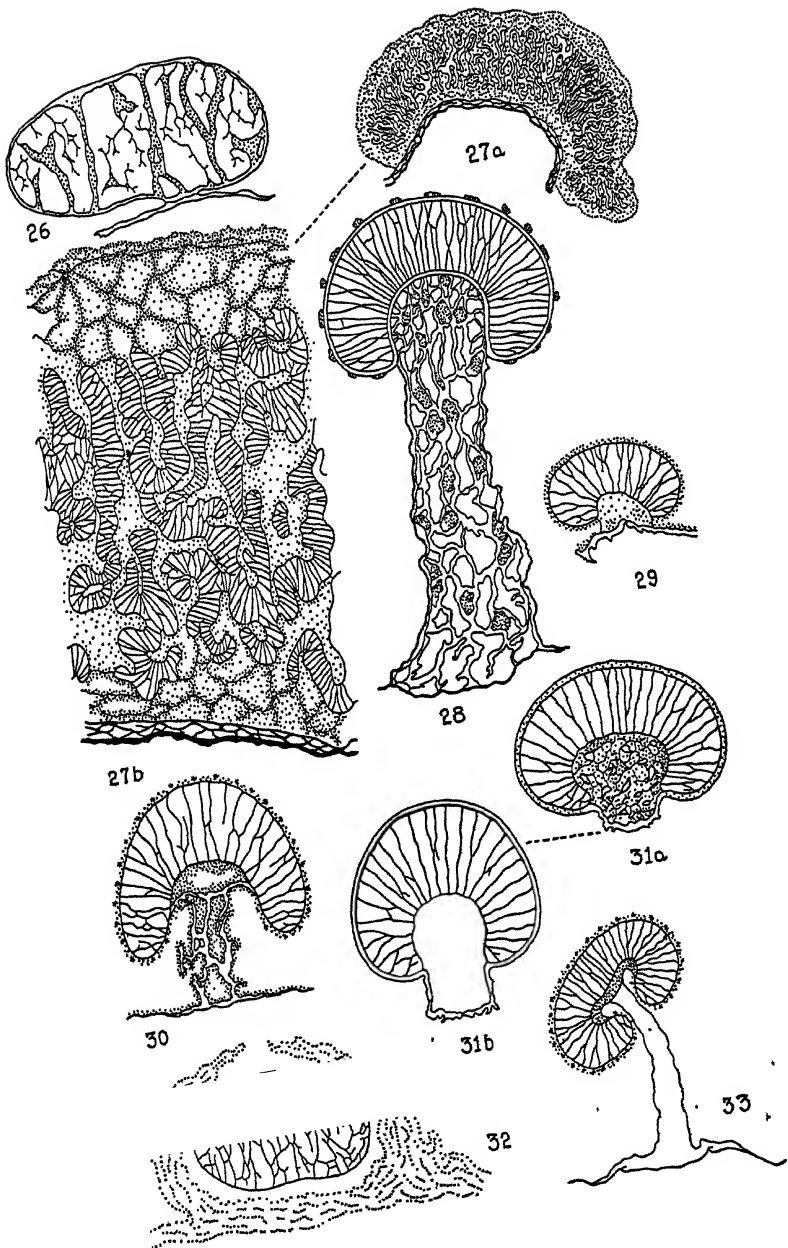


PLATE V

- Fig. 34. *Enerthenema melanospermum* Macbride and Martin. Section of a sporangium. $\times 30$.
- Fig. 35. *Diachaea leucopodia* (Bull.) Bost. Section of a sporangium. $\times 48$.
- Fig. 36. *Comatricha nigra* (Pers.) Schroet. Section of a sporangium. $\times 68$.
- Fig. 37. *Enerthenema papillatum* (Pers.) Bost. Section of a sporangium. $\times 48$.
- Fig. 38. *Diachaea cerifera* G. Lister. Section of a sporangium. $\times 48$.
- Fig. 39. *Comatricha sulsdorffii* Ellis and Everh. Section of a sporangium. $\times 25$.
- Fig. 40. *Stemonitis fusca* Roth. Section of a sporangium. $\times 18$.
- Fig. 41. *Stemonitis axifera* (Bull.) Macbride. Section of a sporangium. $\times 15$.

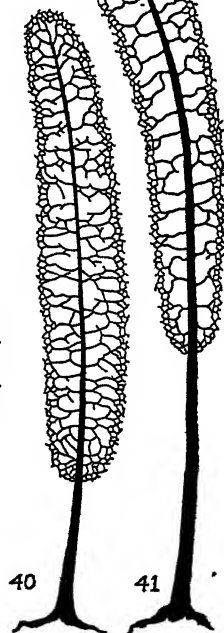
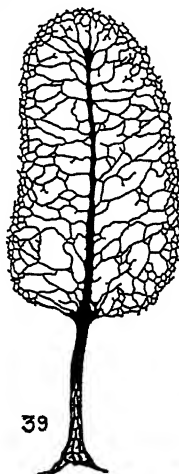
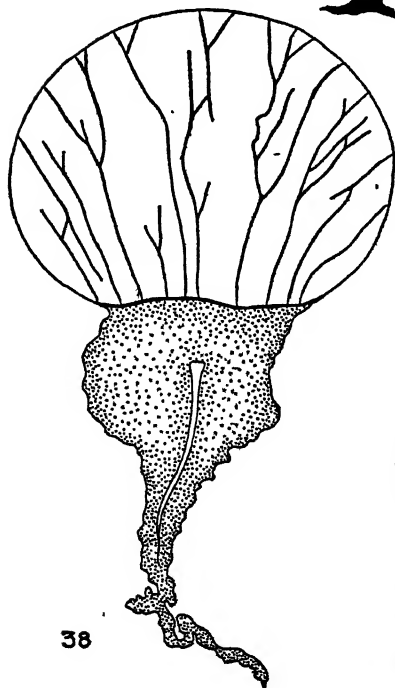
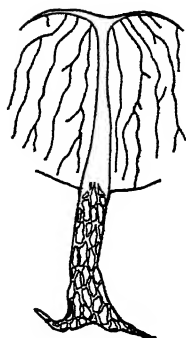
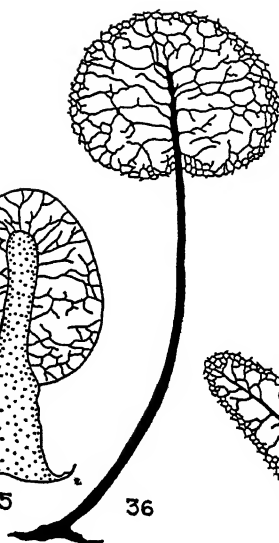
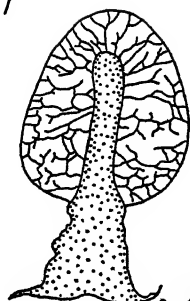
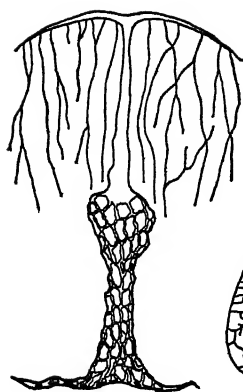
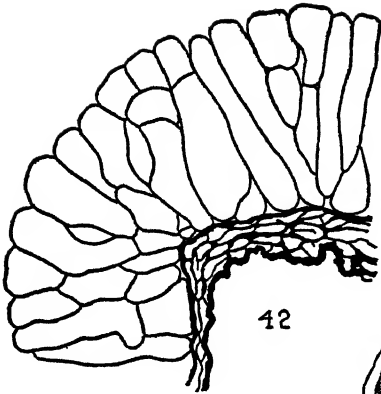
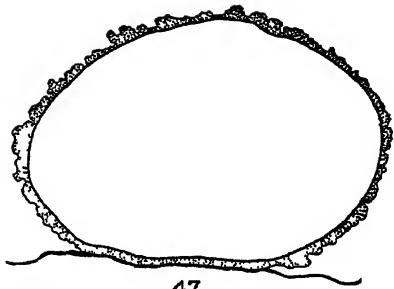


PLATE VI

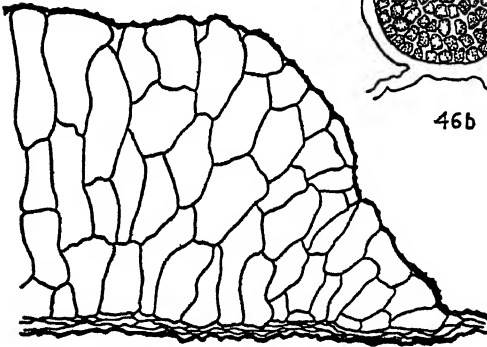
- Fig. 42. *Lindbladia effusa* (Ehr.) Rost. Section of a pseudoaethalium. x 15.
- Fig. 43. *Tubifera ferruginosa* (Batsch) Gmelin. Section of a pseudoaethalium. x 7.
- Fig. 44. *Enteridium splendens* (Morgan) Macbride. Section of an aethalium. x 7.
- Fig. 45. *Licea minima* Fries. Section of a sporangium. x 48.
- Fig. 46. *Licea biforis* Morgan. a. Sections of sporangia. x 48. b. Section of sporangium, with diagram of spore arrangement. x 235.
- Fig. 47. *Licea variabilis* Schrad. Section of a sporangium. x 48.
- Fig. 48. *Lamproderma aroyrionema* Rost. Section of a sporangium. x 48.
- Fig. 49. *Lamproderma violaceum* (Fries) Rost. Section of a sporangium. x 48.



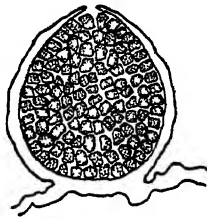
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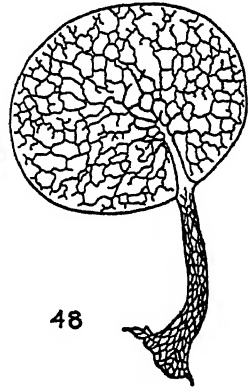
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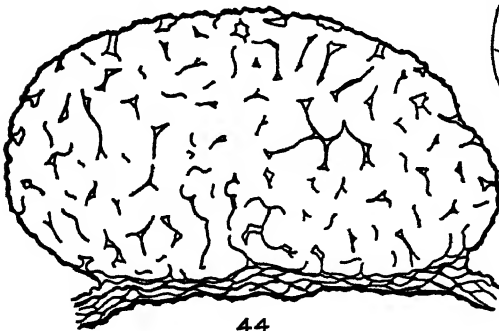
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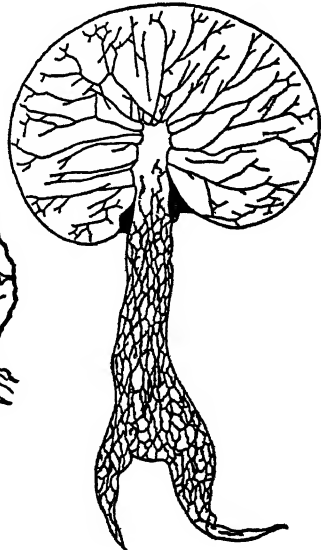
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46a

PLATE VII

- Fig. 50. *Lycogala epidendrum* (L.) Fries. a. Section of an aethalium. x 25.
b. Detail of walls showing origin of capillitium. x 235.
- Fig. 51. *Perochaena depressa* Libert. Section of a sporangium. x 48.
- Fig. 52. *Arcyria cinerea* (Bull.) Pers. Section of a sporangium. x 18.
- Fig. 53. *Cribraria argillacea* Pers. Section of a sporangium. x 48.
- Fig. 54. *Arcyria denudata* (L.) Wettstein. Section of a sporangium. x 48.
- Fig. 55. *Listerella paradoxa* Jahn. a. Section of sporangium. x 102. b. Detail of wall showing the margin of a lobe and point of attachment of two capillitial threads. x 525.
- Fig. 56. *Lindbladia effusa* (Ehr.) Bost. Section of a fructification with distinct sporangia. x 15.

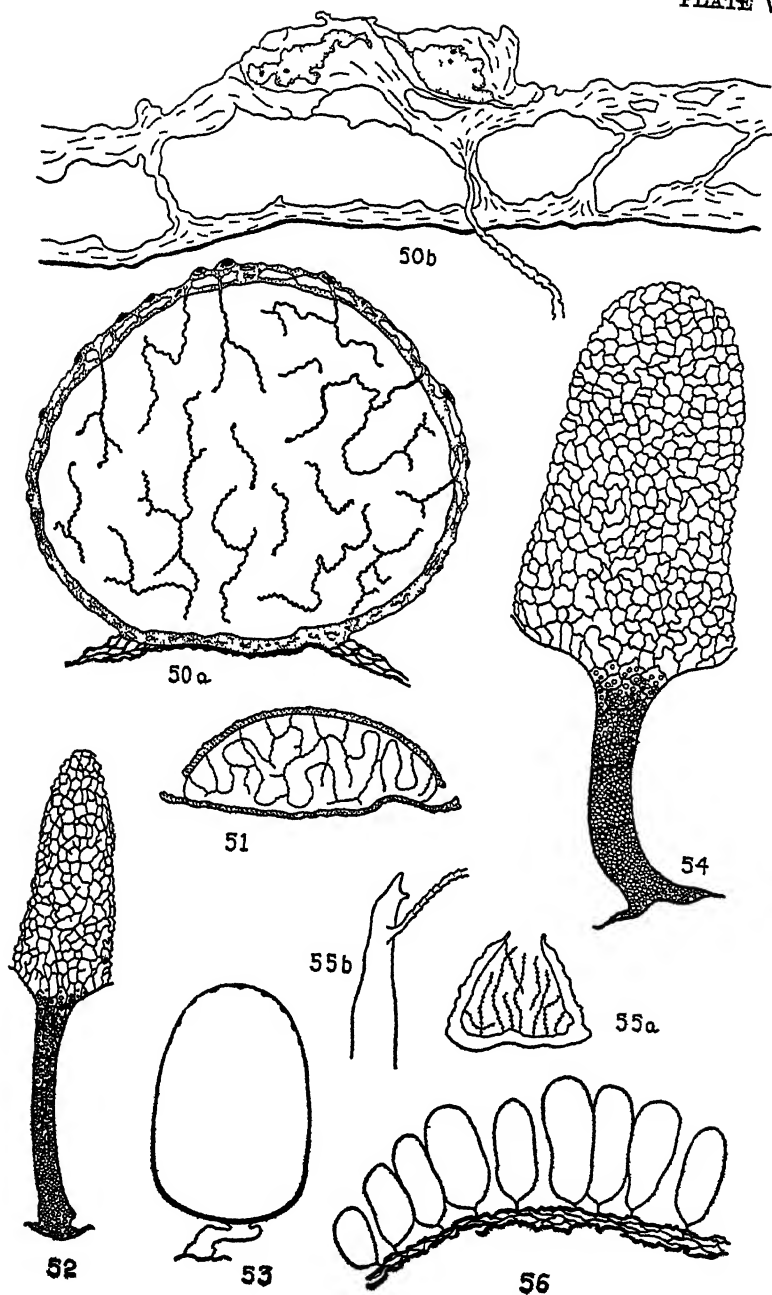


PLATE VIII

- Fig. 57. *Dictydiaethalium plumbeum* (Schum.) Rost. Corner of an immature sporangium showing uncleaved protoplasm and threads. $\times 885$.
- Fig. 58. *Dictydiaethalium plumbeum* (Schum.) Rost. Mature pseudoaethalium in section, diagrammatic. $\times 15$.
- Fig. 59. *Dictydiaethalium plumbeum* (Schum.) Rost. a. Cross section of threads and wall from immature fructification. $\times 1550$. b. Cross section of threads without wall attached, from mature form. $\times 1550$.
- Fig. 60. *Dictydiaethalium plumbeum* (Schum.) Rost. Pattern of threads as seen in cross section near the top of a mature fructification. $\times 135$.
- Fig. 61. *Dictydiaethalium plumbeum* (Schum.) Rost. Cross section of a young sporangium with threads attached to the wall. $\times 525$.
- Fig. 62. *Dictydiaethalium plumbeum* (Schum.) Rost. Section of mature sporangia, enlarged to show threads and caps. $\times 102$.

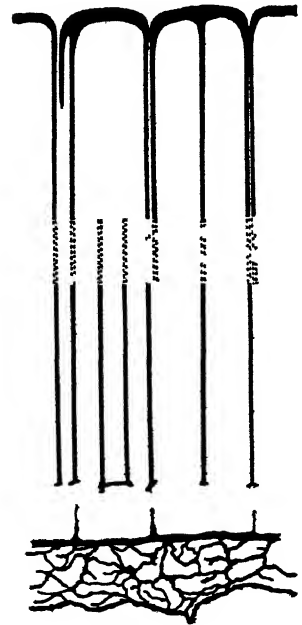
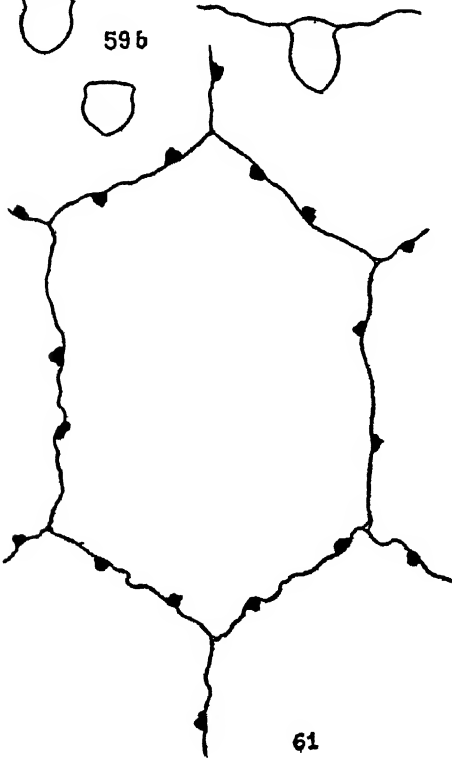
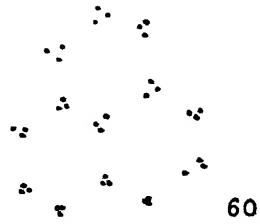
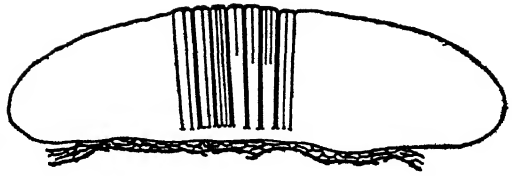
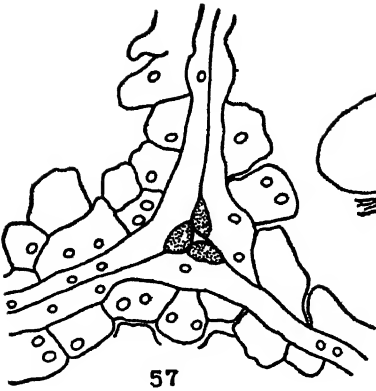


PLATE IX

- Fig. 63. *Margarita metallica* (Berk. and Br.) Lister. Section of a sporangium. $\times 48$.
- Fig. 64. *Ophiotheca vermicularis* (Schw.) Massee. Section of a sporangium. $\times 48$.
- Fig. 65. *Oligonema nitens* (Libert) Rost. Section of a sporangium. $\times 48$.
- Fig. 66. *Arcyria globosa* Schw. Section of a sporangium. $\times 48$.
- Fig. 67. *Hemitrichia vesparium* (Batsch) Machride. Section of sporangia. $\times 30$.
- Fig. 68. *Hemitrichia clavata* (Pers.) Rost. a. Section of a sporangium, elongate type. $\times 30$. b. Section of a sporangium, subglobose type. $\times 15$.
- Fig. 69. *Ophiotheca wrightii* Berk and Curt. Section of a sporangium. $\times 48$.
- Fig. 70. *Hemitrichia serpula* (Scop.) Rost. Section of a sporangium. $\times 48$.
- Fig. 71. *Trichia varia* Pers. Section of a sporangium. $\times 48$.

